GROWTH-HABITS OF MONOCOTYLEDONS — VARIATIONS ON A THEME

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In studying various families of Monocotyledons (as represented in Malaya) during the past twenty years, I have been struck by the very uniform basic growth-pattern among the great majority of these plants, a pattern which yet can give rise to such a variety of growth-forms: bamboos, bananas, pandans, tufted and single-stemmed palms, sedges and grasses, epiphytic and terrestrial orchids and aroids, corm-forming and bulb-forming geophytes, etc. The growth-forms of Dicotyledons, though more varied in detail, are in general much less precisely defined, and so do not display such a conspicuous and distinctive variety.

In the course of my teaching, in presenting the contrast between Monocotyledons and Dicotyledons, I have been led to think about the uniformity of basic growth-pattern of the former, and of its connection with anatomical characters, especially with the absence of a cambium. It appears to me that this viewpoint has been inadequately expressed in text-books of botany, and I have tried to present its essential features simply in the second and third chapters of my book on plant life in Malaya (Holttum, 1954). I also made a short communication on the subject to Section K of the British Association in 1952 (unpublished). In the present paper I am attempting to present the subject more fully, with reference to all the more important families of Monocotyledons, especially those familiar to me in Malaya, whether wild or cultivated.

The examples chosen in the present paper are illustrative, not exhaustive. Much more work might be done on the subject, and taxonomists in particular might find distinctive features hitherto not considered in basic schemes of classification. In looking through taxonomic treatments of some of the smaller families of Monocotyledons, I have been struck by the occurrence of such terms as " acaulescent " and " rootstock fibrous ", which are indications of lack of thought and of observation. As a particular example, there is at present in print no exact description of the vegetative branching habit of the genus *Orchidantha* (Lowiaceae), and only very recently a description of the very precise branching of the inflorescence in that genus (Lane, 1955, Fig. VIII, p. 129).

In looking through former literature for a comparative treatment of the kind now presented, I have come across a paper by Sargant (1903), which contains the record of much careful observation of great value. Sargant was, however, working in a temperate climate, with the idea of adaptation to a seasonal rest as a necessary feature of the majority of plants. Looking at the matter from an equatorial standpoint, I would present a generalization which is diametrically opposite to hers.

Sargant's view of Monocotyledons in general is that they lost their cambium because it was not necessary; that the production of underground perennating organs was facilitated by a cambium-less growth and that the necessity for the production of such organs, therefore, led to the disappearance of cambium. I would suggest, however, that the lack of cambium led first to a peculiar type of continuous vegetative growth in the moist

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tropics, namely sympodial growth, and that this sympodial growth proved itself peculiarly adaptable to the production of resting organs, thus allowing cambium-less plants to spread to seasonal climates.

As Bews (1925) has pointed out for African plants, adaptations to seasonally or continuously dry climates can be shown to be specialized developments of more general growth-patterns shown by plants of the moist tropics. This I believe to be true for plants in general; and though a particular growth-form, such as that of bamboos, may have originated in a monsoon climate, it seems to me probable that the basic sympodial growth-pattern, which is a necessary consequence of the structural limitations of Monocotyledons, originated in a climate of continuous growth.

Dicotyledons and Monocotyledons

Since I originally drafted the present paper, Corner's concluding remarks on the Durian Theory have appeared (Corner, 1954), in which the growth-habits of Dicotyledons and Monocotyledons are compared with little consideration of the limitations imposed by lack of a cambium. I suggest that such a comparison is of limited significance. The significant comparison is surely between woody Dicotyledons and those Monocotyledons which *have* developed a cambium. These latter (a small minority) are almost all included in Hutchinson's Agavales. Another example is the genus *Nivenia* (Iridaceae), which forms strange miniature trees with Iris-like foliage; so that a cambium appears to have evolved on at least two lines among Monocotyledons, and perhaps more than two. All these plants are pachycaul, in Corner's sense. Assuming the validity of Corner's general argument in proposing the Durian Theory, my conclusion would be that a cambium evolved in Monocotyledons relatively later, so that there has been no time for the fully leptocaul stage to arise among them, though the much-branched largest forest trees of *Dracaena* come quite near to the leptocaul condition. Corner objects to the term anomalous as applied to the secondary growth of Agavales; but it must at least be admitted that it is some-

thing basically different from anything in Dicotyledons, and I think it must also be admitted that it arose *de novo* in plants having only scattered closed vascular bundles in their stems.

It may well be true, as Worsdell suggests (1915, 1919), that Dicotyledons have evolved from plants with a primary stem-structure of scattered vascular bundles; but it seems to me also clear that either these primitive Dicotyledons also already had a cambium (almost all known gymnospermous plants, including *Medullosa* among the Pteridosperms, had a cambium), or that they evolved a cambium at a very early stage, much earlier than any Monocotyledon. There are certainly far more variants of behaviour in the cambium among Dicotyledons than any student of the ordinary text-book of botany would realize, and it may be that cambium has also evolved more than once among Dicotyledons; but I suggest that the early possession of a cambium is the prime feature which has permitted the evolution of the leptocaul tree, and that its lack imposes limitations which have resulted in the development of the sympodial habit in its manifold manifestations.

It is with the great majority of Monocotyledons, which lack a cambium, that I am concerned in the remainder of the present paper.

Growth-limiting Characteristics of Monocotyledons and their Effects

The basic limitation is due to lack of a cambium. There may be, locally, groups of cells which retain for a time the power of continued division and increase in size (a particular case of this is intercalary growth, further mentioned below), but there is no zone of cells which continue division indefinitely and no formation of additional vascular tissue nor of additional mechanical tissue once growth in width of a stem is complete.

A consequence of the lack of cambium is that adventitious buds, whether for the production of shoots or roots, are strictly limited; such buds are formed at the nodes and do not subsequently form elsewhere. At each node there is normally one axillary bud which can develop into a new stem

(or inflorescence); if this bud is destroyed, no further bud develops at the node in question, as every orchid-grower soon discovers. The only apparent exceptions to this known to me are the numerous buds which arise on detached scales of a lily bulb, and similarly the groups of small corms at the base of a *Gladiolus* corm; I have not seen a study of the origin of these. At each node of a stem near the ground (or below ground) one or more (often many) roots may develop, but roots are not formed on extended internodes.

An immediate consequence of the lack of cambium is that the primary root, not having the power of increasing in thickness, and of necessity small in origin, is soon too small in cross-section to transmit (even if by branching it could absorb) all the water needed by the growing shoot. The need for further roots then arises, and these can only be adventitious from nodes on the stem, and each root in its turn is limited in its water-conducting capacity by its initial size.

The growth of the stem is, therefore, limited by the number of roots which can be borne at the lower nodes of the stem, these nodes being either below the surface of the ground, or just above the surface (roots arising from nodes much above ground level need to have some protection against drying, and are a special adaptation in some cases). Short internodes in the basal part of the stem are, therefore, a necessity if the plant is to produce a large leaf-area.

Short internodes are also necessary for another reason. The stem-meristem of the embryo is small, and must increase in width as the size of the plant increases. As there is no cambium, this means that the base of the stem is an inverted cone, the width of which increases until the maximum stem-diameter is attained. This inverted cone must be supported by roots growing from the nodes, and for stability the cone must be as short vertically as possible. Hence the necessity for close nodes in this part of the stem.

When the maximum stem-diameter has been attained, and the stem has begun to grow in height by the production of longer internodes, the growth of the plant is limited by two factors: the strength of the basal part of the stem, and the amount of vascular tissue in the basal part of the stem (assuming that there are enough roots at the basal nodes to supply all the water which can pass along the vessels in the stem). The length of life of such a plant is limited. If it produces branches, and these branch again, bearing an increasing number of leaves the demand for water will ultimately be equal to the possible supply. If the stem remains unbranched, with a terminal group of leaves which remain constant in number (as in many palms), the stem ultimately becomes unstable owing to lack of strength, and any damage whatever to vascular tissue (which cannot increase in quantity) will gradually weaken the growing top of the stem. If the stem is unbranched and flowers at the apex, its growth automatically ceases.

All this assumes that the base of the stem remains single; i.e. that no lateral branches are produced. But there is a bud at each of the closely placed basal nodes, and when the growth of the first stem reaches the limiting stage (or even before that), the growth of one of these buds can continue the life of the plant. As the new stem from the bud begins growth, it repeats the same process as the original stem which started from the embryo; it produces a number of short internodes, the nodes thus all close to the ground and having the power to produce new roots, and the diameter of the stem also increasing to its maximum. The new growth is inevitably slightly horizontal at first, to carry the branch growing-point clear of the original stem.

More than one such basal lateral bud may grow, so that the plant may have a tuft of stems. Eventually all the buds on the original stem will have grown or have become inactive through age, but there will be new basal buds on the new stems, and these can continue the growth of the plant, each producing first a region of close root-bearing nodes, and then an erect leaf- and flower-bearing stem. In this way, though the life of any single stem is limited, the growth of the plant as a whole is unlimited (Fig. 1). By contrast, even the largest dicotyledonous tree has a limited life-span.
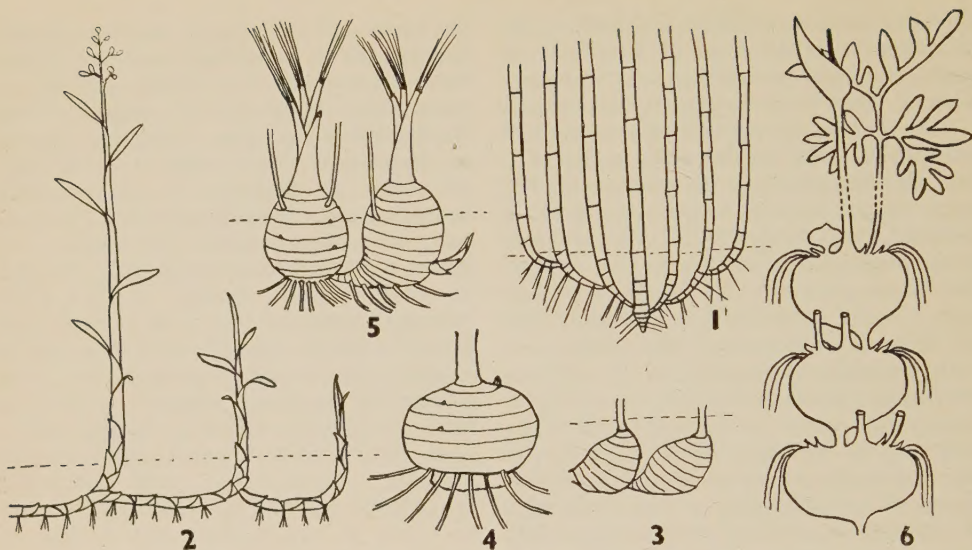
FIGS. 1-6 — Fig. 1. Branching from basal nodes of successive stems, forming a tufted growth. Fig. 2. Regular rhizomatous growth; rhizome sympodial, each erect stem ending in an inflorescence. Fig. 3. Fleshy sympodial rhizome, adapted for resting in dry season. Fig. 4. *Gladiolus* corm (outer sheaths removed), showing old corm at base, and bud (near top) which will form next year's corm. Fig. 5. Two pseudobulbs of *Spathoglottis*, each bearing leaves and peduncles, with growing bud which will form next pseudobulb. Fig. 6. Branching pattern of *Amorphophallus* (after Meusel); the inflorescence is terminal on a corm.

This kind of irregular sympodial growth, each plant forming a tuft of stems, each stem of limited growth, the tuft itself persisting for an indefinite period, might well develop in a tropical climate in which continuous growth is normal. Greater efficiency would be produced if each new stem produced a longer horizontal growth in its early stages, bringing the new erect leafy stem well clear of the former ones, and also allowing the new roots to penetrate to new ground.

Such a habit would lend itself to the development of resting phases, and so to the invasion of zones of seasonal climate in which continuous growth is impossible. The necessary adaptations merely are that each new horizontal growth should arise from an underground bud, and should continue underground, and that this underground part should develop adequate storage tissue. In the unfavourable (dry or cold) season the leafy shoots could die, leaving the underground parts of the stem to rest until the next growing season, when new buds could develop from the nodes and each new shoot could produce its own new root-system. This kind of development has occurred in many families of Monocotyledons, and has led some botanists of temperate regions to think that it is the normal and original form of growth of such plants. To an equatorial botanist, however, the habit of seasonal resting appears as a special development which could have evolved from the evergreen condition of the moist tropics. In each family of Monocotyledons special developments have taken place, some to suit the tropical forest, some to suit open country in seasonal climates, some to produce adaptations to epiphytic growth in varying climatic conditions. In the remaining part of this paper, some of these special developments are discussed. Comparable developments have, of course, also occurred among Dicotyledons, but the majority of these have some cambium development, which allows greater flexibility in growth-habit; the growth-patterns of most such plants are much less precise than among Monocotyledons.

Intercalary Growth

In almost all Monocotyledons the basal part of each leaf forms a sheath which surrounds part of the stem above the node to which the leaf is attached (commonly the attachment encircles the stem). In many cases this sheath is very rigid, and protects the stem which it surrounds. The sheath commonly grows to maturity while the stem beyond the attachment of the sheath remains in an immature and delicate condition. The presence of such sheaths in fact permits the continued growth of the stem in a way which would be impossible without such protection. Under these conditions intercalary growth has developed, the basal part of each internode, protected by the leaf-sheath, continuing to form new cells and push the matured distal part of the internode forwards. This kind of growth is familiar in grasses. It occurs in many other Monocotyledons, and reaches its most striking development in the growth of a new culm of a bamboo plant. Here the sheaths are very rigid, and overlap, permitting very rapid extension in length of the delicate culm-tissues, such extension occurring simultaneously over a series of internodes; only when the full new growth is completed, do the sclerotic tissues of the stem complete their development, after which the protective sheaths are no longer necessary.

The long rigid sheaths of Monocotyledon leaves also sometimes permanently take the place of the mechanical outer tissues of a stem, the true stem remaining soft and delicate. Such a condition occurs in many Zingiberaceae, and in Musaceae. In *Musa*, the leaf-sheaths at first form a pseudo-stem, the true stem remaining very short, at the base of the plant; the true stem ultimately grows up inside the pseudo-stem and bears the inflorescence at its apex.

This protection of young stems, or of permanently delicate mature stems, by leaf-sheaths, is almost universal among Monocotyledons, and it appears to me to be an adaptation directly related to the lack of a cambium.

Corner (1954) remarks that distichous phyllotaxis is the arrangement best suited to internodal extension, and in this he is doubtless right; but he does not mention in this connexion the species of *Calamus* (with spiral phyllotaxis) which have internodes as long as most bamboos. Though a distichous arrangement may be an advantage for facilitating internodal extension, such extension of a large stem would not be possible without the support of leaf-sheaths.

Irregular Sympodial Growth

This occurs in many Monocotyledons of the moist tropics. Because it is irregular, a precise description of the growth-habit of any such plant is difficult, though differences in habit as between different species may be quite distinctive. The most striking examples known to me are in the genus *Pandanus*; they are notable partly because of the large size of the plants, and partly because of the presence of stout stilt- or strut-roots.

In *Pandanus* the inflorescences (whether male or female) are always terminal, but in most species inflorescences are not abundant, and branching is mostly not related to flowering. Some species have normally a single stem from the base, branching above, the whole made stable by the growth of strut-roots in the form of a cone round the base of the stem. In such cases the branching stems may ultimately become too heavy for their bases to support, and breaking occurs, which may be made good by new branches from dormant buds. Probably some pandans of this habit have a limited life. Species which produce new branches from the base of the plant are more efficient; in others heavy branches are made stable by the development of stilt-roots at some distance from the main stem, and by this means indefinite irregular branching at some distance above ground is possible (e.g. *Pandanus labyrinthicus*).

A very different group of plants are the terrestrial orchids of the Goodyera tribe which grow in equatorial forests. These have creeping leafy stems which ultimately end in an erect inflorescence, growth being renewed from a bud near the base of the erect part of the stem. Such orchids often vegetate for considerable periods

and their growth-patterns are quite irregular. Little has been published in the way of careful observation of the growth-habits of these plants.

The Musa Habit

Here each stem is of limited growth, terminating in an inflorescence, and new stems grow in a close tuft round the bases of the old ones, the buds which form such stems often arising at or above ground-level. The middle part of such a tuft gradually decays, growth occurring at the periphery. Ultimately the new lateral buds on the outer stems may well be above ground level, so that rooting is less efficient. In cultivation practice, the plants would not be allowed to reach this stage. I have seen no record of the behaviour of wild *Musa* plants under these circumstances; possibly some outer stems may fall and so bring their basal buds into a more favourable condition for root development.

Some perennial grasses (e.g. the larger species of *Pennisetum*) have a similar habit, and in cultivation become weak after a time because the new shoots originate well above ground level; breaking up of the clumps and re-planting are then necessary when the plants are grown for forage purposes. Sugarcane affords a similar case.

As noted above, greater efficiency of growth for the plant as a whole is obtained where each new stem begins horizontally, bending upwards when its tip is well clear of former growths. This occurs in varying degrees in many different Monocotyledons, and these form transitions to the next type of growth. Among bamboos, all stages of the progression may be seen; but bamboos have also other peculiarities and are dealt with separately below.

Regular Rhizomatous Growth, with Terminal Inflorescences on Erect Stems

The essential feature here is that each new stem-forming bud arises underground, and produces first a horizontal length of rhizomatous stem bearing sheaths at the nodes, rooting at any node, the end of the stem turning upwards sooner or later and producing a (usually unbranched) leafy portion which normally ends in an inflorescence; new growth comes by the development of one or more buds from nodes near the base of the erect part of the stem (Fig. 2).

This is the typical growth-form of the Zingiberaceae of tropical forests. The length of horizontal rhizome produced by each new growth is characteristic of each species, and naturally causes differences of habit (as does also the height of the leafy stems). The rhizome is not primarily a food-storage organ (though food may be stored in it) and is certainly not a resting organ. It is a means whereby a single plant may cover a considerable area of ground, and may continue to spread indefinitely, its growth being continuous. The rhizome of an old plant is always sympodial, formed by the initial parts of a series of new growths, never monopodial.

A feature of many Zingiberaceae is the specialization of new growths as either vegetative or flowering, not as both. The vegetative shoots have a limited growth but no terminal inflorescence. The flowering shoots have no leaf-blades (the leaves are sheaths only, on closely placed nodes) and are usually short, sometimes so short that only the distal parts of the flower-tubes project above ground level, the ovaries and the fruits formed from them remaining underground. A strange case is that of *Hornstedtia grandis*, in which the rhizome, covered by its sheaths, is raised two or three feet above ground level by means of stilt-roots, as if the plant wanted to raise its short inflorescences above the ground, and could not do so by elongation of the peduncles.

There can be no doubt that the primitive habit of Zingiberaceae is that shown by *Languas galanga*, in which all inflorescences are terminal on leafy stems. The dimorphous condition occurs in most of the subdivisions of the family; occasionally both conditions may be found on the same plant (*Zingiber officinale*, and a species of *Costus* in cultivation in Singapore). Specialized short flowering stems have usually retained large primary in-

florescence-bracts, but such bracts have almost disappeared from some species of the *Alpinia* alliance, in which the inflorescence develops almost to maturity inside the protective sheaths of the upper leaves.

Rhizomes as Resting Organs

The rhizomes of forest gingers of continuous vegetative growth are always more or less fleshy, and doubtless they store food which is used when a bud begins to make a new length of rhizome; such new growth is bound to be periodic, though often it occurs before the previous new leafy growths are completed, and its incidence is not necessarily connected with any change of season.

Probably such a plant will behave differently under different climatic conditions, though it would have a limit to its tolerance of dry weather. It may be that the same species in southern Malaya has new rhizome-growth quite irregularly, controlled primarily by the growth of former parts and not by seasonal change, while in northern Malaya it is strictly seasonal in growth, forming new rhizomes (and consequently leafy shoots) in the wet season and not in the drier part of the year. The transition from such behaviour to the total loss of leafy shoots in a prolonged dry season is not a sharp one, and one can imagine that species in a climatic transition zone such as that of northern Malaya might produce mutants fully adapted to a resting stage (Fig. 3); such mutants could then migrate into the monsoon region.

Plants of *Kaempferia pulchra* (native in the north of Malaya and regions still further north) are quite continuous in growth in Singapore, though they rest leafless in the dry season in their natural habitat. Other species of *Kaempferia* (e.g. *K. rotunda*) have become more specialized, and even in the continuously moist climate of Singapore they undergo periodic rest. Within the genus *Zingiber* also are some species of continuous growth, some adapted to a resting period.

The same kind of development has occurred in a number of other families of Monocotyledons besides Zingiberaceae (e.g. Iridaceae). The example commonly quoted in English text-books of botany is Solomon's Seal (*Polygonatum*); but the fact that its growth is sympodial is not always noted. Other examples are *Arum maculatum* (Meusel, 1951) and *Cyperus rotundus*.

Corms of Gladiolus, Crocus, etc.

A corm in the genera *Gladiolus* and *Crocus* is a short segment of rhizome which grows erect, bearing a single terminal leafy (and flowering) stem, and stores food for the next season's growth (Fig. 4). During this new growth the old corm shrivels, and the new corm, produced on top of it (from one of the axillary buds on the old corm), is pulled downwards into the original position by contractile roots.

The only essential difference between a corm of *Gladiolus* and a pseudobulb of such an orchid as *Spathoglottis* (Fig. 5) is that a new *Gladiolus* corm is produced by one of the buds near the apex of the old one, whereas in *Spathoglottis* a new pseudobulb is formed from a bud near the base of an old one, so that contractile roots are not necessary. The essential structure of a *Spathoglottis* pseudobulb and a *Gladiolus* corm is the same, except that normally *Spathoglottis* does not bear a terminal inflorescence (exceptionally it does, especially in hybrids of cultivation). There is, of course, also the difference that most species of *Spathoglottis* are evergreen, but a few are deciduous (e.g. *S. affinis* of Java and northern Malaya).

Meusel (1951) gives a diagram showing the sequence of growth in *Amorphophallus* (Araceae); from this it is evident that the large tubers of *Amorphophallus* are of essentially the same morphological nature as the corms of *Crocus* and *Gladiolus* (Fig. 6).

Bulbs of Amaryllidaceae and Liliaceae

A bulb of the family Amaryllidaceae has the same kind of branching as a corm, each inflorescence (or solitary flower) being terminal, the new bulb (or continuation of the axis of the same bulb)

being formed from a subapical axillary bud. In the bulb, the stem remains short and small, the storage organs being the swollen bases of certain leaves. Different leaves act as foliage leaves, as storage leaves (or as both) and as protective sheaths, and the precise number and sequence of these in each new growth of the sympodium varies in different species. The position of the bud which is to continue the sympodium has always a definite relation to the inflorescence, just as it has in the case of some sympodial Araceae.

Bulbs which are evergreen, such as *Zephyranthes* as cultivated in Malaya, may have a main axis which is vertical and sympodial (Fig. 7), the food-storing leaves functional at any one time belonging to more than one element of the sympodium (see Kerling, 1941). The same is also true of some bulbs which are not evergreen (e.g. *Hyacinthus*, see Blaauw, 1920, Fig. 7). In other cases, a completely new bulb may be formed for each successive resting season. It is, of course, also possible for other axillary buds to form new bulbs (sometimes small ones, at the base of the main bulb): this is comparable to the branching of a rhizome of a species of Zingiberaceae by development of two buds instead of one, near the base of the last leafy stem. The same thing occurs in orchids such as *Dendrobium* and *Cattleya*.
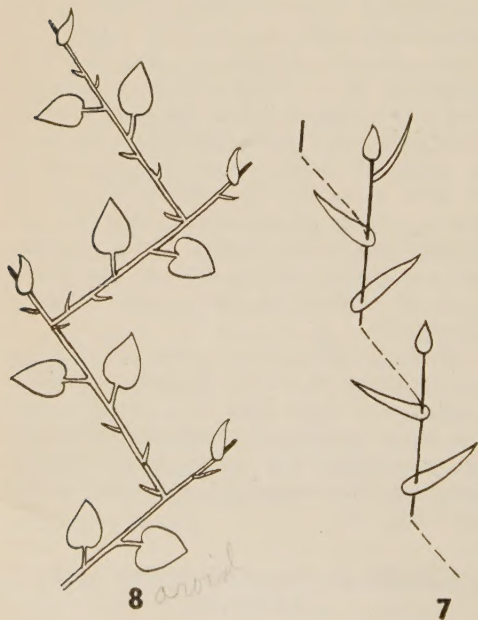
Palms with Terminal Inflorescences

There are comparatively few palms which have terminal inflorescences, one being the Sago palm (*Metroxylon sagus*). This has a rhizomatous habit, like that of plants previously described, and each erect leafy stem is of limited growth, ending in a vast branched inflorescence (Fig. 9). The food stored in the stems (extracted by man as sago) serves in part to form the inflorescence and fruits, in part for new rhizomatous growth. I suggest that this is the primitive growth-habit in palms, and that the type now most abundant, with exclusively axillary inflorescences, is a derivative.

Another genus which has tufted stems (i.e. sympodial growth) is *Arenga* (some species of this genus, notably *A. sacchari-fera*, have single stems only). The apex of an *Arenga* stem forms a rather small inflorescence, and then other (sometimes larger) inflorescences form in the axils of successive leaves downwards (Fig. 10). This genus thus combines the terminal inflorescences of *Metroxylon* with the axillary inflorescences of the majority of palms, and it is an interesting intermediate case.

Another remarkable case is that of *Plectocomia*, a very large rattan (climbing palm) in which there is a terminal inflorescence on each stem (the stems are tufted). The inflorescence is actually a composite one, having branches in the axils of the upper leaves, as in *Pandanus*. A similar condition is also found in the rattan-genus *Korthalsia*; but in the great genera *Calamus* and *Daemonorops*, which provide most of the useful rattans, the growth of each stem is indefinite, all inflorescences being lateral.

The genus *Corypha*, in which there is a single trunk bearing ultimately a terminal

FIGS. 7, 8 — Fig. 7. Pattern of branching of *Zephyranthes* bulb (after Kerling). Fig. 8. Growth-habit of climbing aroid (after Meusel); each new growth has first 2 reduced leaves, then 2 foliage leaves, 2 more reduced leaves, and terminal inflorescence (spathe and spadix).
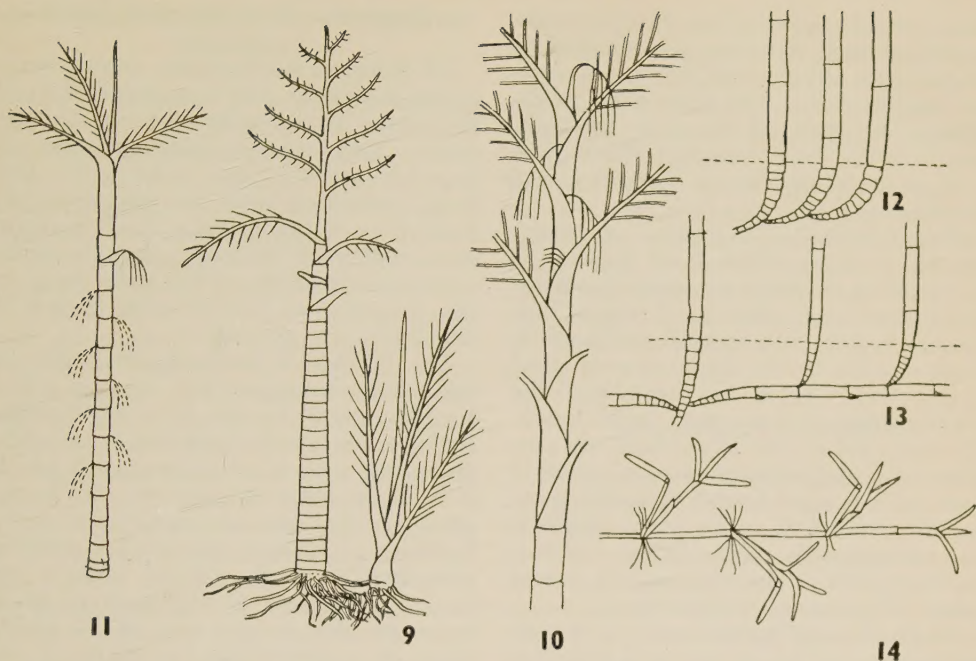
Figs. 9-14 — Fig. 9. Growth-habit of *Metroxylum sagus*. Fig. 10. Top of an *Arenga* palm, showing terminal inflorescence, and other inflorescences in leaf-axils in downward succession. Fig. 11. Habit of an areca palm, an inflorescence in the axil of each leaf (flowers expanding after leaf has fallen); former inflorescences dotted. Fig. 12. Sympodial branching of *Bambusa*, etc. Fig. 13. Monopodial runner of *Phyllostachys* type bearing erect stems formed from lateral buds (after Takenouchi). Fig. 14. Monopodial runner of a panicoid grass (seen from above).

inflorescence, should in my opinion be regarded as derived from palms of the *Metroxylon* habit, by suppression of the basal buds on the stem; this idea is further elaborated in the next section.

Nipa is a rhizomatous palm which bears peculiar (apparently reduced, and certainly very Pandan-like) inflorescences on short stems. Whether these inflorescences are terminal on branches of a sympodium or axillary, has apparently never been decided. The whole problem of the morphology of *Nipa* is of great interest, but very difficult to investigate owing to the large size of the plant and the conditions of deep mud in which it grows.

Palms with Indefinite Apical Growth and Lateral Inflorescences

All the plants hitherto discussed have (at least potentially) terminal inflores-cences, which limit the growth of succes-sive elements of the sympodium. These elements are roughly of similar size, the size being characteristic of each species. Most palms, however, have indefinite apical growth, and all axillary buds (except the lowest ones) form inflorescences (Fig. 11). Many such palms consist of single trunks, among them being the well known coconut palm, so that the single stem is commonly thought to be characteristic of palms. But most palms of the equatorial forest, including almost all the numerous rattans, the genera *Licuala, Pinanga, Areca, Cyrtostachys, Oncosperma, Geonoma, Zalacca* and others (representing many tribes of palms) are tufted (i.e. sympo-dial) in growth. Ridley (1907) publish-ed a paper on this subject.

It appears to me that the sympodial growth-form with apical inflorescences is primitive among palms, as among other

Monocotyledons, and that the indefinite growth of each stem, by development of lateral buds as inflorescences, is a secondary modification. The other main modification of habit in palms of indefinite growth is the development of plants with a single stem (see note on *Corypha* in the previous section).

It is notable that in genera (or groups of allied genera), where some species are tufted and some single-stemmed, the latter species have larger trunks. I suggest that the single stem is a special modification, made possible by the suppression of basal lateral buds, which has permitted the development of one very large trunk. The existence of this large trunk has permitted the single stems of such palms to grow to a greater height than the great majority of tufted palms (*Oncosperma* is an exceptionally tall tufted palm). Corner (1954), however, would regard palms as primarily monocaulous.

Single-stemmed palms must be propagated by seeds; but if one could stimulate the suppressed basal buds to develop, vegetative propagation would be possible, and this might be of great assistance in the breeding of such palms, two of which are of great importance in world economy (Coconut and African Oil Palm).

But whether single-stemmed or tufted, palm stems of indefinite apical growth must ultimately die because of the mechanical considerations mentioned in the introductory sections of this paper.

It might be possible for a single-stemmed palm, having fallen through lack of strength of the lower part of the trunk, to continue to live by forming adventitious roots from some of the upper nodes (as regularly occurs with some Marantaceae, and as I recently saw in the case of a fallen *Cycas* trunk in the forest in Pahang). But probably in such palms specialization has proceeded so far that roots cannot be formed (or not quickly enough) at such upper nodes, where normally they would not grow. However, it is interesting to note the practice in Egypt of causing date palm trunks to root some distance above the ground, for purposes of propagation of good varieties (Täckholm & Drar, 1950).

Bamboos of Sympodial Habit

All Malayan bamboos are strictly sympodial in growth, but they differ from all the plants so far considered in various ways, chiefly in the large number of branches borne by the erect stems, this being correlated with the comparatively small size of the leaves. Each bamboo stem is strictly limited in growth, being attenuated upwards, in this differing from the majority of palms; each branch is also limited in growth.

The flowers of bamboos are borne on the smaller branches, and in most cases on every small branch of a single culm. Perhaps this is an extension from the state of having a terminal inflorescence which is found in the great majority of Gramineae. In that case, the condition of many bamboos in Malaya represents a possible reversion; in these plants flowers are casually produced at the ends of small leafy branches on any part of the plant. There is no doubt that the centre of distribution of bamboos in Asia is the monsoon belt; as one travels southwards in Malaya, the number of bamboo species diminishes. This southward migration may have occurred only among such species as could adapt themselves to such casual flowering. I know of no recorded case of native Malayan bamboos flowering gregariously and then dying, as is the habit of many bamboos in the monsoon region (a plant may be considerably weakened by the full flowering of several culms, but may yet gradually regenerate from small basal buds).

The hollow internodes of bamboos are a particular adaptation providing maximum strength from a given amount of tissue; this adaptation may also perhaps be in part responsible for the rapid growth of bamboo culms (the rigid culm-sheaths, as mentioned above, are the main factor in this development). The hollow internodes appear to have no other special correlation with growth-habit.

All the bamboo genera which are generally considered to be most primitive in flower-structure have a strictly sympodial habit (*Schizostachyum* and allied genera, *Dendrocalamus*, *Gigantochloa* and *Bambusa*).

Gramineae which have Monopodial Runners

Some bamboos (e.g. *Phyllostachys*) and a great many grasses have horizontal runners of indefinite monopodial growth, these runners bearing erect leafy and flowering stems which grow from lateral buds on the runners (Fig. 13). This is a quite different growth-habit from the sympodium of the larger bamboos (Fig. 12), in which each erect culm is terminal, and any lateral spreading is by short lengths of rhizome the ends of which turn upwards. Takenouchi (1931) reports that in *Arundinaria* (or *Indocalamus*) *niitakayamensis* some rhizomes are wide-spreading, turning up at length and giving rise to separate tufts of erect stems.

The tufted habit of sympodial bamboos is, of course, matched by the many grasses which have a tufted habit. There are a few grasses which have subterranean and strictly sympodial rhizomes like those of a bamboo or ginger (e.g. *Panicum repens*), but in general the creeping grasses have monopodial runners (Fig. 14), which are commonly leafy and not subterranean (bamboo runners are subterranean). Indeed, in some cases the runners are supported well above the ground by stilt-roots (e.g. several small panicoid grasses in Malaya).

Among tropical grasses the two main growth-habits are (a) tufted and (b) creeping by monopodial runners. The annual habit is a development from (a) adapted to climates with a long dry season. It is an important habit, because the cereal crop-plants of today have been derived by selection from such grasses. In Malaya, some introduced " annual " grasses occur as weeds of open ground (e.g. *Eragrostis* spp.); they can regenerate from seed at any time, so are no longer annuals, and they can only be clearly distinguished from their perennial relatives of similar habit by careful observation. I do not find the monopodial creeping habit clearly defined in most taxonomic works dealing with grasses, and I suggest that a further study of grasses with this idea in mind would be worth while.

The inflorescence of grasses is (so far as I know) always terminal on a leafy stem. Sometimes each erect shoot bears one inflorescence; the case of such a single inflorescence with ample paniculate branching is probably to be regarded as primitive among grasses (e.g. *Phragmites*, *Panicum*, *Saccharum*) and is also found in the bamboo genus *Arundinaria*. But the panicled inflorescence of *Phragmites* is already a highly specialized development, and needs comparison with the condition of *Bambusa*. In some ways, as one might expect, bamboo inflorescences are more primitive than those of any grass.

Monopodial Orchids

The great majority of orchids, especially of epiphytic orchids, are strictly and very regularly sympodial in growth. There may be a specialization of vegetative and flowering branches (e.g. in *Coelogyne* and allied genera) which is comparable to the condition of many Zingiberaceae, but this is developed as part of the basic sympodial pattern.

By ensuring that each new stem has its own new set of roots, the sympodial growth-habit is clearly of value to epiphytes, for which the problems of water-supply and secure attachment to the supporting tree are of paramount importance. But plants of a tufted habit are localized. By limiting each leafy stem to one leaf, and by the development of considerable lengths of rhizome between successive leaves, the genus *Bulbophyllum* (among others) has produced plants which can spread along the branches of trees and so tap new sources of water and nutritive material (Fig. 15). Other orchids have developed a similar result by the abandonment of the sympodial habit.

In the majority of sympodial orchids, the basal part of each new growth is specialized for root-bearing (its leaves are commonly reduced to sheaths), and roots do not (in some cases certainly cannot) grow on the distal part of each stem, which is specialized to leaf-bearing and flowering. The apex of each new stem of, e.g. *Dendrobium* has a limited growth. If the apical part of such a stem is planted as a cutting for purposes

of propagation, new growth comes by the development of lateral buds, the new growths from which each have their own roots.

In the case of the Sarcanthine orchids, each stem-apex has the power of unlimited growth, and necessarily correlated with this is the power of producing roots at all nodes of the stem, not only the basal ones. An orchid plant of this habit, if it has fairly long internodes (e.g. *Arachnis*), can climb from the bottom of a tree-trunk to the top, and still have roots near its growing point (Fig. 16). In the process of such a climb, the growing stem-apex moves from conditions of shade and humid atmosphere to lighter and drier conditions; in some cases, it can only flower when it reaches full sunlight. Such a habit then permits the seedling to grow in a more sheltered position than is demanded by the mature plant (compare the behaviour of *Gleichenia*, prothalli of which grow in a sheltered place, the rhizome of the sporophyte spreading to greater exposure). *Arachnis* plants, one of which may form a thicket by irregular branching, each branch continuing indefinitely in growth, may scramble over small trees, or over rocky cliffs, where the necessary conditions of exposure are found.

But not all orchids are adapted to grow and flower in conditions of full exposure, and among monopodial orchids of the *Vanda* alliance are many which are adapted to moderate shade. A long-climbing stem would not be appropriate in such cases, and in fact a great many of these orchids have rather short internodes; they even adopt almost a sympodial habit by branching irregularly near the supporting tree, but each such branch can continue indefinitely in growth, having no fixed limit as in the strictly sympodial orchids (these plants approximate to tufted palms in habit). Plants of *Aerides*, *Thrixspermum*, *Sarcanthus*, etc., have an irregularly bushy habit, the weight of the continually growing stems often making them pendulous. In a few cases, e.g. *Schoenorchis micrantha*, the individual stems are short, erect, and root near the base only, so that, to a casual glance, they do not differ significantly in habit from *Dendrobium*;

but each stem-apex can continue indefinitely in growth.

The most remarkable cases of reduction in these monopodial orchids are seen in the genus *Taeniophyllum*, plants of which have very short stems of slow growth, the closely placed leaves reduced to minute scales in the axils of which grow the slender inflorescences (Fig. 17); the work of photosynthesis is carried out by roots. Plants of *Phalaenopsis*, many species of *Sarcochilus* and other genera also have very short internodes, with closely overlapping leaf-sheaths, the stem increasing in length very slowly, the plants branching little and remaining very compact (Fig. 18).

The other cases of monopodial growth in orchids known to me are in the genus *Dipodium* (allied to *Cymbidium*), and in two genera of a very different branch of the orchid family, namely *Vanilla* and *Galeola*. In both cases, there are regularly sympodial species, with limited growth of each new stem, closely allied to the monopodial ones; but there are no obvious near allies to the Sarcanthine orchids, which form a very distinct and also a very numerous group of genera, all of which are exclusively monopodial.
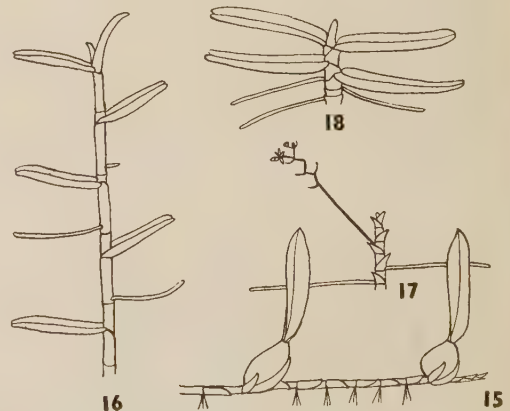
FIGS. 15-18 — Fig. 15. Growth-habit of *Bulbophyllum*, each rhizome-element ending in a pseudobulb of one internode, bearing one leaf. Fig. 16. Top of *Arachnis* stem, showing adventitious roots. Fig. 17. Diagram of top of *Taeniophyllum* stem, showing scale-leaves, roots, and an inflorescence. Fig. 18. Monopodial stem with short internodes (Sarcochilus type).

I recently discovered by chance a single case of potential monopodial growth in the genus *Dendrobium*, all other species of which known to me are sympodial, with every new stem of limited growth. The species in question is *D. lobbii*, which grows on the ground in stream-beds liable to occasional flooding, in full sunlight. I found that a stem-tip of this, cut off and put into a closed propagating frame, continued to grow at the apex and to produce roots from the upper nodes, exactly in the manner of *Arachnis* or *Vanda*.

Water-storage in Epiphytic Orchids

In the case of terrestrial Monocotyledons which rest from growth in the unfavourable season, the above-ground green leafy shoots normally die completely, the rhizomatous first part of each element of the sympodium remaining below ground, and serving as a store of food for new growth. In the case of epiphytes, no part of the plant is protected in the same way as an underground rhizome. Furthermore, the need is for storage of water rather than for the storage of food, especially in the case of evergreen epiphytes which need to survive for periods of days or even weeks without rain.

Almost all evergreen epiphytic orchids have a water-store in the leaf-bearing parts of the stem, or in the leaves themselves, or in both, not in the root-bearing rhizome. In the case of the monopodial Sarcanthine orchids, the storage is inevitably in the leaves. A further consequence of their monopodial habit is that they cannot be entirely deciduous; enough leaves must remain to protect the necessarily large apical bud (none of them produces specialized scale-leaves for this purpose). Such orchids are thus not well adapted to live in climates with a very severe dry season, and they abound especially in the equatorial regions. Some species, native of seasonal climates (e.g. *Vanda insignis*), which normally stop growth in the dry season, will grow continuously when brought to a continuously wet climate like that of Singapore, but they may not flower well.

Deciduous sympodial epiphytic orchids commonly store food and water in the leaf-bearing parts of the stems, which are decidedly fleshy; the stems are protected by the sheathing leaf-bases, which remain when the blades have fallen (the blades are always jointed to the sheaths). Such water-storing leafless stems may be long and of an even thickness (e.g. many species of *Dendrobium*) or short and more or less bulb-shaped (whence they are all commonly called pseudobulbs). In the genus *Bulbophyllum* the last internode of each new growth alone is fleshy and bears (in Malayan species) a single leaf. I know of no epiphytic orchid in which the rhizomatous part of each new element of the sympodium forms a water-store. In the case of some epiphytic members of the genus *Hedychium* (Zingiberaceae) the principal water-store is in fleshy roots.

Marantaceae

Most plants of Marantaceae have a sympodial branching, in which each new shoot is limited to a few internodes, sometimes to a precise number (*see* Holttum, 1951). On any branch, arising from an axillary bud, the first leaf (very close to the parent axis) is a two-keeled prophyll. The next leaf, very close to the first, is a sheath with no blade. Next is commonly another very short internode, and at the end of it a normal foliage leaf. In the genus *Donax* there are one or two more leaves, spaced at internodes of varying length, and a terminal inflorescence (not always developed).

Buds in the axils of the lowest leaves may soon start growth and form new branches of the same kind, and buds in the axils of the lowest leaves of these new branches may repeat the process, thus forming a close tuft of shoots, each of a few internodes. In *Donax*, the penultimate internode of a strong shoot may be more than two metres long, and at its apex will develop a close tuft of branches, each of which will in turn flower, fruit, and ultimately fall, leaving a scar. Ultimately this tuft of branches may become too heavy for the long slender internode of the parent stem, which then falls to

the ground (often it is supported for a time by neighbouring plants). The new shoots arising from basal buds on such a fallen tuft will put out roots into the ground, and so the plant renews its growth, ultimately again putting up stems with long internodes to bear fresh tufts of branches high above ground level.

There are many variants on this pattern within the family Marantaceae, depending on the number of leaves on each new shoot and on the position and length of the long internodes. In most Marantaceae the development of a close tuft of branches in a position raised above ground level is confined to the inflorescence (e.g. *Phrynium, Calathea*).

In some climbing Araceae (e.g. *Rhaphidophora, Anthurium, Philodendron*), there is a similar very precise sympodial habit, each branch bearing exactly (or almost exactly) the same number of leaves (often only one is a foliage leaf, the rest being sheaths only, or bracts) with the same sequence of internodelengths, sometimes one internode much longer than the others (Meusel, 1951), the growth of a new element of the sympodium arising in the axil of the penultimate leaf (Fig. 8). As noted above, the same branching pattern is found in the bulbs of some Amaryllidaceae.

Dioscorea

In the genus *Dioscorea* a great variety of underground storage organs have evolved; in some species a still greater variety has been developed by man in the course of cultivation and selection over a very long period. The morphology of these storage organs is complex, and their mode of development peculiar. They do not show nodes and internodes, nor well-marked sheathing leaves, and their modes of growth are not obviously a development of the basic sympodial Monocotyledon pattern, though I think they probably are in fact a development of that pattern.

There is one group of species of *Dioscorea* in which the underground part is rhizomatous, with horizontal growth (often branching) of which the old parts gradually die away. These species would

appear to be nearest the general Monocotyledon plant in their growth-habit, and a study of them might lead to a clearer understanding of the peculiar developments found in other species. This can only be done by comparative study of living plants in cultivation. Prain & Burkill (1936) remark of *Dioscorea* in general that " the relation of the new shoot to that of the previous season offers a little-explored field ".

Mr E. Milne-Redhead has recently shown me at Kew a very remarkable dwarf species of *Costus* (Zingiberaceae) from Rhodesia, *C. spectabilis*. The rhizomes formed by this species, instead of growing horizontally, grow vertically downwards; they form resting organs, and persist during the dry season in which the green above-ground parts of the plant wither. When the rains come again, new growth comes from a lateral bud near the top of the vertical rhizome; the rhizometip does not grow further. This habit reminds me very much of the downwardgrowing tubers of some species of *Dioscorea*; these tubers also regenerate from buds near the top. The *Dioscorea* tubers are not morphologically exactly equivalent to the downward-growing rhizome of *Costus spectabilis*; but perhaps the *Costus* gives an indication of the way tuber-evolution in *Dioscorea* may have started. In any case, these *Costus* rhizomes give an interesting variant on the normal sympodial growth-pattern in Zingiberaceae.

Summary

A sympodial habit of branching is almost universal in Monocotyledons. The significance of this habit in relation to the lack of a cambium is discussed. Some variations of detail within the sympodial pattern in different groups of Monocotyledons are considered, and it is shown that such different growth-forms as those displayed by climbing aroids, bulbous Amaryllidaceae, and corms of Iridaceae are all modifications of the same basic pattern of branching. Departures from the sympodial pattern in Palmae, Gramineae and Orchidaceae are also discussed.

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FLORAL DIMORPHISM IN *COMMELINA FORSKALAEI* VAHL AND *C. BENGHALENSIS* L.

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Introduction

Cleistogamous flowers have been recorded in the following plants of the family Commelinaceae: *Tradescantia erecta* Jacq. syn. *Tinantia fugax* Scheidm (Henslow, 1879), *Commelinantia pringlei* (Tharp, 1927; Parks, 1935), *Commelina virginica* (Uphof, 1934), *C. nudiflora* (Calvino, 1922, 1923) and *C. indehiscens* (Barnes, 1949).

The aerial and underground flowers of *C. forskalaei* have been described by Hagerup (1932) and Trochain (1932). A similar study has been made on *C. benghalensis* by Trochain (1932), Maheshwari & Singh (1934), and Barnes (1949). Some of our observations differ from those of previous authors and are summarized below.

Material

C. forskalaei is apparently a new record from the north Indian plains. On the Delhi Ridge the plant (Fig. 1) is common in sandy depressions during and for some time after the rainy season disappearing by the end of November. *C. benghalensis* is even more abundant being found everywhere in moist shady places during the rains.
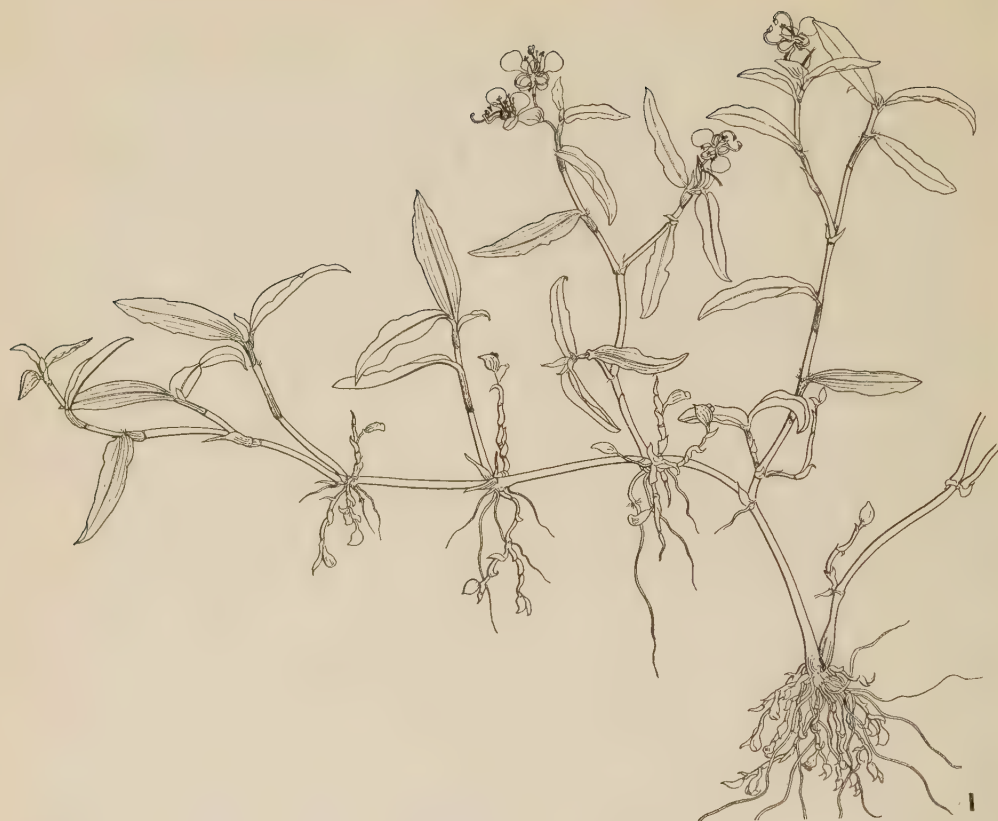
Fig. 1 — Habit sketch of *Commelina forskalaei* showing aerial and underground flowers. × ¾.

Many plants of both species were examined in the field for two successive years, 1954 and 1955. These observations were supplemented from herbarium specimens and fixed material. Pollen grains were stained with a mixture of 50 per cent glycerine and acetocarmine. Pollinated stigmas, kept overnight in 5 per cent KOH (50°-55°C), were stained with acetocarmine to trace the pollen tubes. Seeds of different sizes from aerial and underground flowers were sown to study their germination capacity.

Observations

Commelina forskalaei Vahl

The flowers borne on the aerial shoots are usually chasmogamous, while those that remain underground are cleistogamous.

Aerial Flowers — There are normally three to five flower buds in a spathe, but only one fruit is formed, rarely two. The flowers open early in the morning and fade at noon (cf. Bowman, 1949, on *Spironema fragrans*). Of the two cyme branches in a spathe, the inner is normally one-flowered (Fig. 2, *A*). This flower (*A*), borne on a long, articulate pedicel, is generally the first to open but is always sterile as in *C. benghalensis* (Trochain, 1932; Maheshwari & Singh, 1934; Barnes, 1949), *C. attenuata*, *C. tricolour* and *C. nudiflora* (Barnes, 1949). In a large majority of cases it is strictly male and soon drops off leaving the stalk behind (Fig. 3, *A*). Occasionally it possesses a pistillode. In *C. jacobii* and *C. undulata*

(Barnes, 1949) the inner cyme branch is reduced to a very short flowerless axis.

The outer cyme branch bears two to four flower buds. Slightly later, or concurrently with the first, the second flower (Fig. 2, *B*) projects out of the spathe. It is bisexual and chasmogamous but self-pollinated and retracts into the spathe soon after pollination. In rare cases the second flower was found to have opened before the first. Concerning the third flower, Hagerup (1932), who describes this species from the arid dunes of Timbuctu, states that it is bisexual, normally fertile and always cleistogamous. Trochain writes the same on the basis of a study of plants growing at Senegal in West Africa. Our observations, however, show some differences. The third flower (Fig. 3, *C*) is *normally chasmogamous* and usually comes out at a stage when the second flower (*B*) is already fertilized and is on its way to fruit formation. Further, it is of variable structure and intergrades from unisexuality to bisexuality with occasional seed setting. Some 300 spathes were examined. In 58 per cent of them it was found to be staminate with an imperfectly developed pistil, as shown in Fig. 3. In addition to the third flower the spathe may also show one or two other flower buds which become arrested and remain bathed in the mucilage. These are usually cleistogamous and staminate, although a small pistillode may sometimes be present. However, in approximately 5 per cent of the spathes even the fourth flower (Fig. 4, *D*) protrudes out of the spathe although it never produces a fruit. In the South Indian commelinas, according to Barnes (1949), the first few flowers on the outer cyme have fertile pistils. After one or more capsules have set, the subsequent

flowers bear pistils showing varying degrees of abortion marked by a progressive shortening and coiling of the style leading to its eventual disappearance. Our study of *C. forskalaei* reveals a similar trend in the third or at any rate in all the subsequent flower buds. In *Commelinantia pringlei* (Tharp, 1927) it is the first flower which opens and develops into a fruit, while the rest drop off.

In one abnormal spathe (Fig. 5), the inner cyme branch showed a leafy hyaline bract and two male flowers; normally it bears usually only one bractless male flower.

The flowers are trimerous. Of the three petals the two posterior are larger, clawed and spreading. The androecium comprises three fertile stamens and three staminodes (Figs. 2, 3). Of the former, one shows a long, curved anther having a yellow-blue colour, while the other two have small, ovate, pale blue anthers. At maturity their filaments become irregularly bent. The three staminodes (Figs. 2, 3) have the form of laciniated, yellow bodies borne on short filaments. In *Spironema fragrans* (Bowman, 1949) all the six stamens are fertile and, by their delicate petal-like connectives, lend a filmy or feathery character to the entire inflorescence.

The microspore nucleus divides to form the tube and generative nuclei separated by a delicate membrane. At the shedding stage the tube nucleus becomes less chromatic and the generative nucleus (Fig. 6) assumes various forms ranging from a sickle to a coiled, twisted or a U-shaped body. The mature pollen grains are spherical to ovoid with a thick exine. The generative cell migrates into the pollen tube and produces two elongated sperms (Fig. 7).

The gynoecium consists of a trilocular, 5-ovuled ovary having a long, curved style. At the time of pollination the filaments of the fertile stamens coil. At the same time the style elongates into a spiral (Fig. 8) and the stigma gets pollinated. The two anticous locules (Fig. 9) contain two ovules each, of which one develops into a dull black, smooth seed (Fig. 10), while the other becomes arrested. At maturity these locules open by a loculicidal valve while the posticous

TABLE 1 — PERCENTAGE FREQUENCY OF SEX DISTRIBUTION IN THE AERIAL FLOWERS OF *C. FORSKALAEI*

Flower	Bisexual	Male	Male with pistillode
1st flower	—	98	2
2nd flower	100	—	—
3rd flower	17	25	58
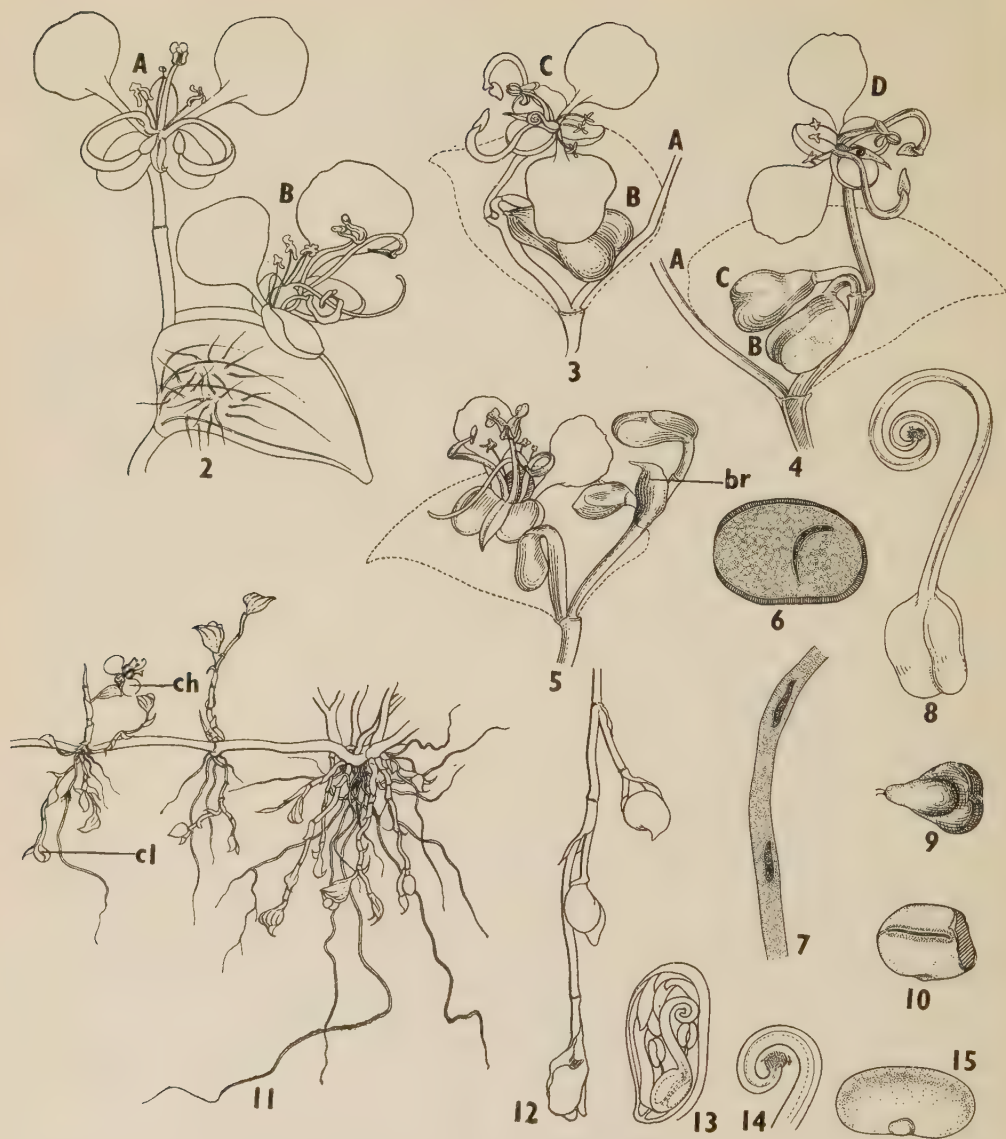
Figs. 2-15 — *C. forskalaei* (*br*, bract; *ch*, chasmogamous flower; *cl*, cleistogamous flower). Fig. 2. Spathe with a staminate *A*, and a bisexual flower *B*, both protruding. × 3¾. Fig. 3. Same, with spathe open. The staminate flower at *A* has dropped off; of the two flowers on the outer cyme branch *B* has matured into a fruit and *C* is open. × 3¾. Fig. 4. The staminate flower at *A* has dropped; the bisexual flowers, *B* and *C* have produced fruits; *D* is male with a pistillode. × 3¾. Fig. 5. An abnormal spathe showing a leafy hyaline bract *br* and two male flowers on the inner cyme branch. × 3¾. Fig. 6. Mature pollen grain with a sickle-shaped generative cell. × 464. Fig. 7. Part of pollen tube from an aerial flower showing the two male gametes. × 464. Fig. 8. Gynoecium showing the coiled style of an aerial bisexual flower seen at time of pollination. × 16. Fig. 9. An aerial 5-ovuled fruit. × 3¾. Fig. 10. A mature seed from the 2-ovuled anticous locules of an aerial fruit. × 7½. Fig. 11. Part of a prostrate branch showing underground cleistogamous flowers *cl* and aerial chasmogamous flowers *ch*. × 1½. Fig. 12. Underground branch with cleistogamous flowers. × 3¾. Fig. 13. L.s. cleistogamous flower showing one large, curved anther, two smaller anthers and a spirally coiled style. × 7½. Fig. 14. Enlarged view of upper part of style of Fig. 13. × 21·5. Fig. 15. Seed produced from underground flower. × 7½.

locule is indehiscent and contains one comparatively larger and oblong seed. Thus the mature capsule has three seeds of which one is larger. The seeds are full of mealy endosperm and contain only a small embryo. As regards their germination capacity, both types of seeds require an approximately similar period for germination. The size difference does not, therefore, seem to affect the germination potential of the seeds.

UNDERGROUND FLOWERS — A very interesting feature is the occurrence of underground cleistogamous flowers both on the rootstock and at a number of nodes (Figs. 1, 11). In contrast to *C. benghalensis* (Burck, 1906), where the underground flowers precede the aerial, here they are produced either simultaneously or slightly later than the aerial flowers. The cleistogamous flowers are borne on whitish branches 3-8 cm long which are provided with scarious leaves usually reduced to their sheathing bases. Some of the branches grow downward in the loose, sandy soil and produce underground spathes developing in the axils of leafy scales (Figs. 11, 12). There is usually a single bisexual flower, rarely two, in each spathe. This flower (Fig. 13) resembles the upper chasmogamous bisexual flowers except for its reduced size, absence of pigment and lack of any clear distinction between the sepals and petals. In the closed flower, elongation of the style results in a spiral coil (Figs. 13, 14) and the stigma is brought in contact with the large, yellow, curved anther (Fig. 13). While a large number of pollen grains germinate on the stigma both in the aerial and underground flowers, a few might do so while still within the anther sac. In comparison to the aerial flowers, which occasionally fail to ripen, the underground flowers are uniformly fertile. The fruits, protected by the chartaceous spathe, contain a single indehiscent seed with a hard testa, instead of one large and two small seeds as in the aerial fruits. The ovules in the other chambers remain undeveloped and ultimately degenerate. The single seed (Fig. 15) is of about the same size as that produced in the posticous locule of an aerial fruit. The underground seeds, which are self-sown in nature, germinate in the laboratory with the same rapidity as the aerial ones.

At Delhi, towards the end of November the night temperature goes down to 10°C. Even the aerial spathes remain closed under such conditions and may occasionally set seeds cleistogamously.

TRANSITIONAL FLOWERS — Some of the branches destined to produce underground flowers fail to grow down due to the presence of rocks or other impediments in the soil. They usually show a single blue coloured chasmogamous flower (Fig. 11). Such transitional types have also been reported in *Commelinantia pringlei* (Parks, 1935) and *Commelina benghalensis* (Barnes, 1949). The spathes produce one or rarely two bisexual flowers on the outer cyme branch while the inner cyme branch is often nonexistent or has the form of a slender flowerless stub.

Commelina benghalensis L.

As already known, this species (Fig. 16) also produces dimorphic flowers borne on the aerial and underground shoots. Our observations differ in some respects from those of previous workers and are, therefore, summarized below.

DISTRIBUTION OF FLOWERS IN AERIAL SPATHES — One to three spathes occur on each axillary inflorescence. The spathes are obconic or funnel-shaped and often differ from one another in size as well as in the number of flowers. The blue or bluish-violet flowers open early in the morning and fade out at noon as in *C. forskalaei*. The inner cyme branch bears a solitary male flower (Fig. 17, *A*) borne on an articulate pedicel as in *C. forskalaei*. This flower is generally the first to open but soon falls off. Sometimes it possesses a pistillode. In smaller spathes the inner cyme branch is either suppressed to a very small axis or is absent.

The outer cyme branch consists of one to three flowers. The first of these (Fig. 17, *B*) comes out of the spathe at the same time or slightly later than the male flower on the inner cyme branch. This is bisexual and chasmogamous but self-pollinated as in *C. forskalaei*. The behaviour of the next flower has been described differently by various authors. Trochain

FIG. 16 — Habit sketch of *C. benghalensis* showing aerial and underground flowers. × ¼.

(1932) describes this species from Senegal and mentions that the third flower is bisexual, self-fertile and cleistogamous. Maheshwari & Singh (1934) report the same from a study of plants growing at Agra. Our observations at Delhi show, however, that the third flower, if present, comes out of the spathe after or sometimes simultaneously with the second (Fig. 18, *B, C*). It is bisexual and self-pollinated but *chasmogamous* (Fig. 19, *C*). A fourth flower, if present, is also bisexual, self-fertile and chasmogamous. Thus one to three capsules may be produced in a spathe although the usual number is two (Fig. 20).

The organization of the flowers is essentially similar to that in *C. forskalaei*. The androecium consists of three stamens and three staminodes (Figs. 17-19). At maturity the staminal filaments become spirally coiled. The gynoecium (Fig. 21)

consists of a three-lobed ovary and a style which is slightly longer than the lateral stamens. The mechanism of pollination is the same as in *C. forskalaei*. However, the style (Fig. 22) and the filaments of the lateral and median stamens are more strongly coiled than in *C. forskalaei*. The anticous chambers, both two-seeded, open at maturity by a loculicidal valve. The posticous locule is indehiscent and contains one seed which is larger than the other four and germinates more quickly. All the seeds are dull, black, wrinkled and provided with spherical excrescences.

CLEISTOGAMOUS FLOWERS — A number of axillary shoots arise from the lower portions of the plant. Many of them penetrate the loose, damp, sandy soil and develop into long runners. There is a single pear-shaped (Fig. 23) spathe in the axil of a leafy scale. It encloses a
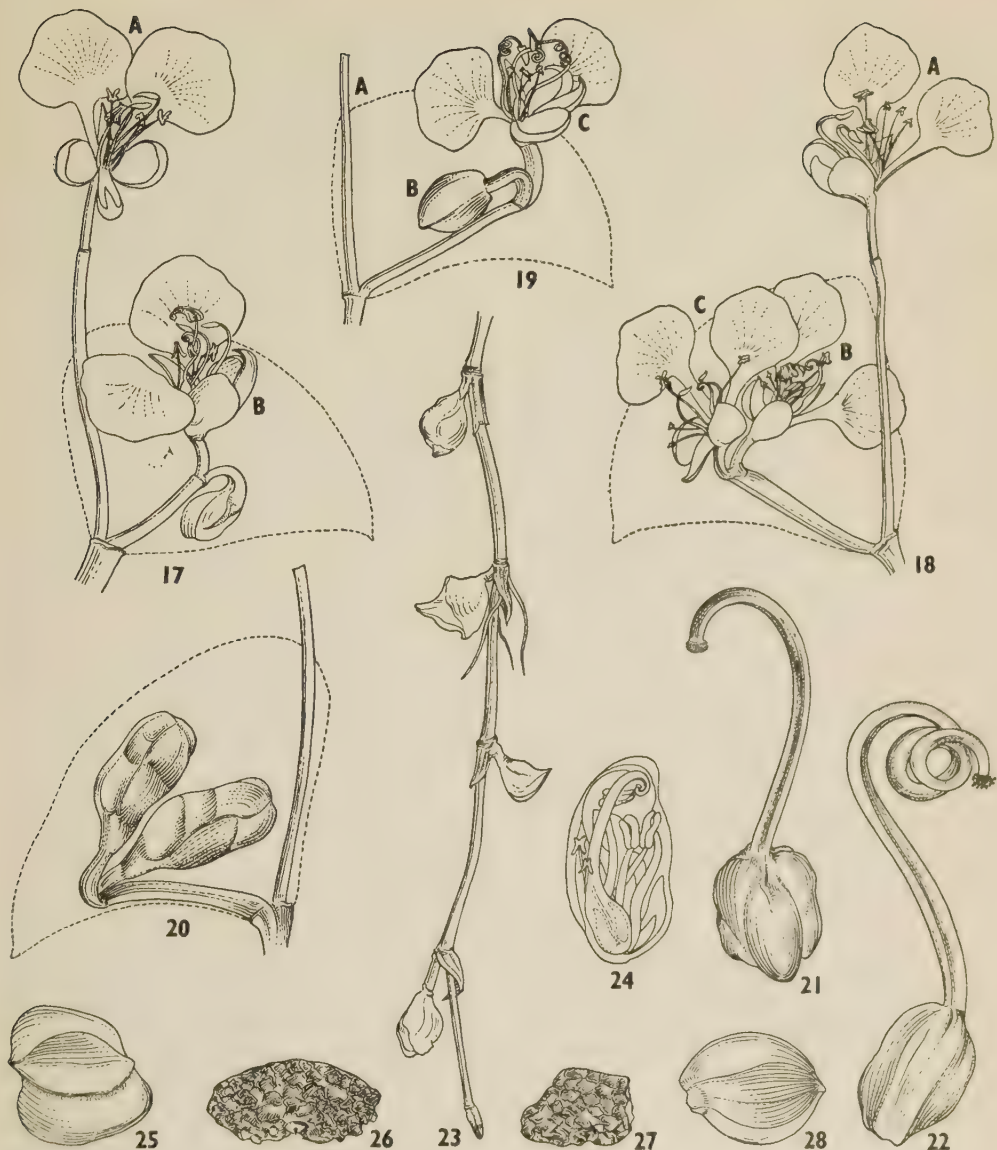
FIGS. 17-28 — *C. benghalensis*. Fig. 17. Spathe with one staminate flower *A*, one bisexual flower *B* and a closed bud. × 5. Fig. 18. Spathe showing the three flowers *A*, *B* and *C*, all in an open condition. × 5. Fig. 19. The staminate flower *A* has dropped; the bisexual flower *B* has matured into a fruit and the bisexual flower *C* has opened. × 5. Fig. 20. Spathe showing two nearly mature fruits. × 5. Fig. 21. Gynoecium showing style before pollination. × 20½. Fig. 22. Same, after pollination. × 20½. Fig. 23. Underground branch with cleistogamous flowers. × 5. Fig. 24. L.s. cleistogamous flower showing a spirally coiled style. × 9½. Fig. 25. A 3-seeded, underground capsule. × 5. Fig. 26. A large seed produced underground. × 9½. Fig. 27. A small seed produced underground. × 9½. Fig. 28. A 3-seeded fruit from a transitional flower. × 5.

solitary bisexual flower (Fig. 24) on the outer cyme branch, the inner branch being absent. The small, bluish petals remain within the sepals. At the time of pollination the style elongates in the form of a spiral (Fig. 24) and the stigma gets pollinated. Numerous pollen grains were seen germinating on the stigma in both chasmogamous and cleistogamous flowers.

The fruits (Fig. 25) usually contain three seeds (occasionally two or four) in contrast to the one-seeded condition in *C. forskalaei*. The seed (Fig. 26) in the posticous chamber is always the largest. This germinates as vigorously as the seeds from the aerial fruits; the two smaller seeds (Fig. 27) showed no sign of germination.

TRANSITIONAL FLOWERS — As in *C. forskalaei*, some of the flowering shoots borne near the base fail to enter the soil. The spathes borne on them resemble the underground ones except for their green colour. In addition, there occur short, green, slender branches, one at a node, bearing two to three smaller, urn-shaped spathes. They contain a solitary, bisexual, self-pollinated flower on the outer cyme branch, the inner cyme branch being absent as in the underground spathes. Such flowers usually remain enclosed inside the narrow-mouthed spathe, although a partial opening may occur sometimes. In branches, which are only partially buried under the soil, the upper portion often curves up and produces capsules above the ground. The solitary fruits (Fig. 28) produced in these spathes are usually three-seeded as in the underground ones.

Discussion

The present observations on the nature of the third flower in the aerial spathes of *C. forskalaei* and *C. benghalensis* show that it is bisexual, self-pollinated and chasmogamous. Previously, Hagerup (1932), Trochain (1932) and Maheshwari & Singh (1934) reported from a study of plants growing in other localities that the third flower is cleistogamous. That environment can bring about a change from cleistogamy to chasmogamy or vice versa has been shown in a number of cases.

Hansgirg (1891) designates such flowers, which remain closed owing to deficiency of light, as photocleistogamous; and those remaining closed due to high water level or strong currents as hydrocleistogamous. Flowers which fail to open due to environmental effects are called " pseudocleistogamous " or " ecologically cleistogamous " (Uphof, 1938). According to Henslow (1879) cleistogamy is brought about in *Tradescantia erecta* Jacq. syn. *Tinantia fugax* Scheidm by low autumn temperatures, and Knuth (1906) describes this as thermocleistogamy. In *Commelinantia pringlei* (Parks, 1935) the cleistogamous flowers, if accidentally or otherwise exposed to light, produce small chasmogamous flowers with purple petals. Similarly, in *Commelina forskalaei* the short basal shoots bearing uniflowered spathes produce a chasmogamous flower (Fig. 11) if unable to enter the soil due to some impediment.

Two hypotheses have been put forth regarding the origin and significance of cleistogamy. Burck (1906) considers this to be genetic and suggests that in many species such a condition might have originated by mutation. As examples may be cited *Ammannia latifolia* and *Salvia cleistogamica* (see Uphof, 1934) in which even under the most favourable conditions the plants failed to produce any chasmogamous flowers. Weatherwax (1929) regards the cleistogamous species *Poa chapmaniana* as having originated from the chasmogamous *P. annua* by mutation or by some selective process. Cleistogamy, according to Weatherwax, is an effective barrier which prevents the new species from hybridizing with its parent. Goebel (1923), Ritzerow (1908) and Uphof (1934, 1938), on the other hand, are of the opinion that cleistogamous flowers represent retarded forms of chasmogamous ones. A man-made cleistogamous-chasmogamous dimorphism has been described by Smith (1950) in *Arachis hypogaea*. Several authors consider this to be a transitional stage between chasmogamy and underground cleistogamy. This view has, however, been criticized by Smith (1950) who attributes the occurrence of the subterranean fruits of *Arachis* to a geocarpic habit. The lowest cotyledonary branch

and the first two lateral branches, which produce inflorescences, here become buried early in the season by cultivation. *Commelina forskalaei* and *C. benghalensis*, however, exhibit a distinct example of this type of floral dimorphism with transitional forms near the soil surface.

In all the members of Commelinaceae there is a reduction of floral parts. In *Commelina* cleistogamy is commonly associated with a reduced size of the flowers, lack of normal colour and fewer seeds per fruit. In *C. forskalaei* the subterranean fruits produce a single seed as compared with the three unequal seeds in the aerial fruits. In some members of the Gramineae (Uphof, 1938; Brown, 1949) and the Malpighiaceae (Uphof, 1938) the cleistogams are so greatly modified that even the correct identity of the plant becomes difficult to establish. *Stipa leucotricha* (Brown, 1949) is an example where the cleistogamous spikelets borne in the axils of lower leaves are considerably reduced. Uphof (1934) reports that in *Commelina virginica* the formation of aerial flowers becomes scarce towards the end of the season but the underground flowers can develop for some time longer and produce fruits. In *Bromus catharticus* (Brown, 1949) also the inflorescences, which are produced late in the spring under dry, hot conditions, contain a larger proportion of cleistogamous florets. A similar condition prevails in *Commelina forskalaei* and *C. benghalensis*, where with the onset of unfavourable winter conditions the plant generally produces more underground than aerial fruits.

Summary

Commelina forskalaei is a common annual at Delhi. It produces blue chasmogamous flowers in the upper part of the stem, smaller transitional flowers near the surface of the soil and cleistogamous flowers under the ground. The aerial spathes enclose two cyme branches. The inner cyme branch bears a single male flower. The second, borne on the outer cyme branch, is bisexual and self-pollinated. The third flower is chasmogamous but shows a variable structure. The spathe possesses usually one, sometimes two fruits. The fruits contain one large and two small seeds.

Cleistogamous flowers are produced on long, etiolated, underground branches. Usually there is a single bisexual flower in every spathe. Pollen grains may germinate within the anther sac. The fruits contain a single seed which is " self-sown ". Underground seeds germinate as quickly as the aerial seeds. Towards the end of the season, even the aerial spathes remain closed and may occasionally set seeds cleistogamously.

C. benghalensis also produces aerial chasmogamous and underground cleistogamous flowers. In the aerial spathes the inner cyme branch, if present, bears a solitary, male flower. The outer cyme branch bears one to three bisexual, self-fertile flowers all of which are chasmogamous. The mechanism of pollination is similar to that in *C. forskalaei*. The fruits contain five, unequal, dull black, wrinkled seeds. The smaller seeds germinate more slowly than the larger ones.

Underground spathes are produced on axillary shoots arising from the rootstock and lower nodes. They enclose a solitary, bisexual flower. The fruits usually contain three unequal seeds.

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L'APPLICATION DE CERTAINES DONNÉES EMBRYOLOGIQUES À LA SYSTÉMATIQUE DES OROBANCHACÉES ET DE QUELQUES FAMILLES VOISINES

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Dans la série des Contortées et la sous-série des Solaninées, les Scrofulariacées, les Gesnériacées, les Orobanchacées et les Bignoniacées sont particulièrement apparentées par leurs caractères floraux et la nature capsulaire de leurs fruits. Elles ne présentent pas, d'après Fritsch (1893) de limites bien précises entre elles et l'on a même souvent hésité à considérer les Orobanchacées comme une famille autonome. Eichler (1875) en a fait une simple subdivision des Gesnériacées et, plus spécialement, une ligne collatérale parasite, mais Hallier (1903), après les avoir réunies primitivement aux Gesnériacées, a pu, finalement, tout aussi bien les rattacher aux Scrofulariacées, avec lesquelles elles présentent, comme l'a démontré Boeshore, en 1920, une continuité morphologique, anatomique et biologique. Aussi, quand Beck-Mannagetta (1895), dans la classification d'Engler & Prantl (1895), s'est rallié au point de vue de l'autonomie des Orobanchacées, on peut se demander s'il n'a pas adopté, ainsi, une simple solution de compromis, bien qu'il ait maintenu sa position en 1931.

Les embryologistes se devaient d'apporter à l'éclaircissement de ce problème de taxinomie, difficile à résoudre en s'adressant aux critères habituellement invoqués, le secours de leur science. Glišić (1929), l'un des premiers, considérant le parallélisme qui existe dans la formation des suçoirs et de l'albumen chez les Scrofulariacées et les Orobanchacées, a admis que les deux familles présentaient entre elles une étroite ressemblance, que, à ce point de vue au moins, elles pouvaient être confondues. Alors que c'est surtout des Rhinanthées que se rapprocheraient les Orobanchacées, c'est plutôt avec les Verbascées, Scrofulariacées réputées généralement primitives, que les Gesnériacées présenteraient le plus de ressemblance. Glišić a eu pour lui le mérite d'être un précurseur dans cette voie, mais il a eu seulement recours à des arguments tirés du développement de l'albumen et, de plus, il n'a disposé, à cette époque, que de renseignements encore bien peu nombreux. L'embryologie des Orobanchacées et des familles qui leur sont apparentées est actuellement beaucoup mieux connue et, surtout, le mode de développement de l'embryon peut être, à présent, pris en considération. Il n'est pas impossible de dégager de ces diverses données un certain nombre de conclusions, qui, malheureusement, ne peuvent être encore que toutes provisoires.

Au cours de ce travail, il sera question d'abord de l'embryogénie, puis du développement de l'albumen chez les Orobanchacées, les Scrofulariacées, les Gesnériacées et les Bignoniacées, enfin du retentissement de ces faits sur nos conceptions de la systématique de ces familles.

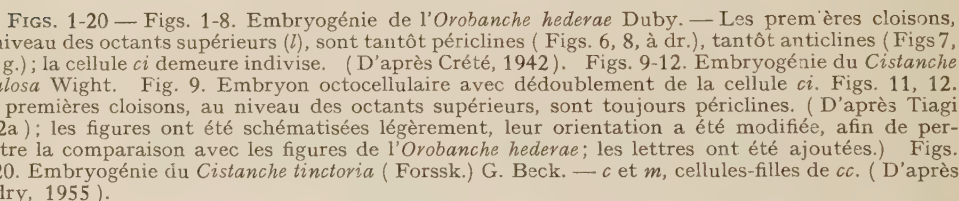## I. Le développement de l'embryon

A. OROBANCHACÉES

C'est à de nombreuses années que remontent les premières observations précises sur l'embryogénie des Orobanchacées: dès 1878, en effet, Koch a déterminé, chez l'*Orobanche hederae*, la marche de la segmentation dans la cellule embryonnaire, assisté à la différenciation des quadrants, des octants, de l'hypophyse, du dermatogène et conclu à l'identité du développement embryonnaire chez les

Orobanchacées et les Crucifères. Cependant il a décrit l'ordre d'apparition des parois sans prendre en considération le nombre des blastomères composant, en réalité, chaque étage et je me suis cru autorisé, en 1942, à reprendre l'étude embryogénique de l'*Orobanche hederae* Duby., en utilisant les techniques modernes de l'investigation embryologique.

L'embryon de cette espèce se rattache au type embryonomique des Crucifères par la présence d'une tétrade filamenteuse en T, appartenant à la catégorie A_2 (Fig. 1) et par les destinées de la cellule basale, qui donne naissance aux initiales de l'écorce au sommet radiculaire, *iec*, au primordium de la coiffe, *co*, et au suspenseur, *s*. Le mode de formation du dermatogène au niveau des octants présente d'intéressantes particularités: les premières cloisons n'apparaissent pas simultanément dans les blastomères (Figs. 5, 6) et, surtout, au niveau des octants supérieurs, elles sont fréquemment anticlines horizontales (Figs. 7, 8) au lieu d'être périclines, comme c'est la règle chez les Crucifères; ainsi le dermatogène se différencie-t-il à un stade ultérieur. Au niveau des octants inférieurs, les cellules circumaxiales, situées sous le dermatogène, se divisent transversalement (Fig. 8 à dr.) et, dans le proembryon contenu dans la graine mûre, ni le périblème, ni le plérome ne sont encore identifiables. L'individualisation de l'hypophyse se fait aux dépens de la cellule *d*, fille de la cellule intermédiaire *m* de la tétrade, soit par division verticale dès le stade des quadrants (Fig. 3), soit par une cloison horizontale, s'insérant sur la paroi qui sépare les octants de la cellule hypophysaire (Fig. 6). Le suspenseur *s. stricto* demeure court: il comprend une cellule assez persistante, soeur de la cellule *d* et une cellule, bientôt écrasée par l'albumen en voie de développement; ce second élément représente la cellule inférieure *ci* de la tétrade (Figs. 1-6).

Chez l'*Orobanche Eryngii* Duby. (Crété, 1942), la tétrade appartient à la série A_2 comme chez l'*O. hederae*; les quadrants se situent de même sur un plan horizontal et la cellule intermédiaire *m* de la tétrade se divise en deux éléments superposés *d* et *f*.

FIGS. 1-20 — Figs. 1-8. Embryogénie de l'*Orobanche hederae* Duby. — Les premières cloisons, au niveau des octants supérieurs (l), sont tantôt périclines (Figs. 6, 8, à dr.), tantôt anticlines (Figs 7, 8, à g.); la cellule ci demeure indivise. (D'après Crété, 1942). Figs. 9-12. Embryogénie du *Cistanche tubulosa* Wight. Fig. 9. Embryon octocellulaire avec dédoublement de la cellule ci. Figs. 11, 12. Les premières cloisons, au niveau des octants supérieurs, sont toujours périclines. (D'après Tiagi 1952a); les figures ont été schématisées légèrement, leur orientation a été modifiée, afin de permettre la comparaison avec les figures de l'*Orobanche hederae*; les lettres ont été ajoutées.) Figs. 13-20. Embryogénie du *Cistanche tinctoria* (Forssk.) G. Beck. — c et m, cellules-filles de cc. (D'après Kadry, 1955).

En 1951, Tiagi a commencé une étude systématique et extrémement précise de l'embryologie d'un certain nombre d'Orobanchacées. Ses observations sur l'*Orobanche cernua* Loeffl. lui ont permis de rattacher l'embryon au type des Crucifères. Les divers stades du développement sont identiques à ceux qui ont été observés chez l'*O. hederae*; cependant, la cellule inférieure ci de la tétrade se divise transversalement et le suspenseur reste plus longtemps identifiable que dans l'espèce voisine. Dans la cellule d, la première cloison est toujours horizontale et ses bords viennent s'appliquer sur la paroi qui limite inférieurement les octants, ou bien encore sur la cloison inférieure du dermatogène de l'axe hypocotylé.

Chez l'*Orobanche aegyptiaca* (Tiagi, 1951), la tétrade appartient également à la catégorie A_2.

Tiagi (1952a) s'étant adressé au *Cistanche tubulosa* Wight., a décrit des formes proembryonnaires une fois encore identiques à celles des *Orobanche*. Cette espèce est toutefois caractérisée par une formation plus régulière du dermatogène; en particulier, les premières cloisons, au niveau des octants supérieurs, ont toujours été figurées en position péricline (Figs. 11, 12). Les octants inférieurs présentent les mêmes destinées que dans les espèces précédentes. L'individualisation de la cellule hypophysaire se fait, une fois encore, aux dépens de la cellule d, soit au moyen d'une paroi horizontale en

forme de verre de montre (Fig. 12), soit à l'aide d'une première cloison verticale (Figs. 10, 11). Le suspenseur *s. stricto* comprend, comme chez les deux Oroban-chacées précédentes, trois cellules qui se résorbent rapidement (Figs. 9-11).

Jusqu'à ces dernières années, on a pu croire, ainsi, que l'embryogénie des Oro-banchacées était extrêmement homogène. C'est Tiagi (1952b) qui a découvert un type embryonomique, nouveau pour la famille, chez l'*Aeginetia indica* Linn. (Figs. 21-32). Normalement, il se forme, dans cette espèce, une tétrade linéaire filamenteuse qui n'appartient donc plus à la catégorie A_2, comme celle des autres Orobanchacées, mais à la catégorie C_2 (Figs. 22, 25). L'embryon octocellu-laire prend naissance par division verticale des éléments *cc*, *cd* et *m* de la tétrade, dont l'élément inférieur *ci*, par contre, se cloi-sonne transversalement en deux cellules superposées, *n* et *n'* (Fig. 28). Ces deux cellules sont rapidement résorbées et, à des stades plus âgés, le proembryon ne comprend plus que les trois étages *cc*, *cd* et *m* (Figs. 29, 31); en Fig. 31, l'étage *cc* est bicellulaire, l'étage *cd* est quadricellu-laire; l'étage *m*, où l'un des blastomères est en voie de division, est à un stade intermédiaire entre les états tricellulaire et quadricellulaire. Tiagi ne s'est pas prononcé sur le type embryonomique auquel peut se rattacher le jeune sporo-phyte de l'*A. indica*; évidemment, les destinées des différents étages peuvent ne pas paraître évidentes, puisque le déve-

loppement complet, à l'intérieur de la graine, aboutit, après des divisions très variables, à un embryon où ne sont diffé-renciés ni la radicule, ni la gemmule, ni les cotylédons (Fig. 32). Cependant, il n'y a pas lieu d'hésiter, à mon avis, sur la présence dans le proembryon parvenu à maturité, des trois étages fondamentaux, partie cotylée, axe hypocotylé où des cloisons verticales ont isolé des éléments du dermatogène, hypophyse où il apparaît, dans certaines des quatre cellules circum-axiales, un cloisonnement oblique. Dans la classification périodique de Souèges (1948), le proembryon de l'*A. indica* se rattache, dans la première période, au mégarchétype IV, par les destinées de la cellule basale du proembryon bicellu-laire, qui donne naissance aux initiales de l'écorce de la racine, au primordium de la coiffe et au suspenseur; il appartient, par sa tétrade linéaire, à la série C et, par le cloisonnement vertical des éléments *cc* et *cd* de la tétrade, à la sous-série a_1, c'est à dire au troisième groupe de la classifica-tion. A côté de cette forme, la plus fré-quente chez l'*Aeginetia indica*, Tiagi a signalé la présence, beaucoup plus rare, de tétrades en T filamenteuses, appartenant à la série A_2, et dont les destinées sont évidemment identiques à ce qu'elles sont chez les autres Orobanchacées (Figs. 23, 24).

Tout dernièrement, Kadry (1955) a décrit, chez le *Cistanche tinctoria* (Forssk.) G. Beck, un développement proembryon-naire tout à fait inattendu chez les Oro-banchacées (Figs. 13-20). Ni la cellule basale du proembryon bicellulaire, ni la cellule *cd*, fille inférieure de la cellule api-cale de ce même proembryon, ne parti-cipent à la construction de l'embryon. Dans la nomenclature proposée par Souèges (1941), le *C. tinctoria* viendrait se ranger dans la troisième période de la classification embryogénique (Souèges & Crété, 1952). La cellule *cc*, soeur de *cd* et petite-fille de l'oospore (Fig. 16), donnerait naissance à deux blastomères superposés *c* (ou *ce*) et *m* (ou *cf*) (Fig. 17) dont l'un, au pôle apical, se diviserait longitudinalement et l'autre, transversale-ment; la tétrade obtenue, tétrade troi-sième, appartiendrait à la catégorie B_2 (Fig. 18). Il est, selon moi, impossible

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Légende générale des figures.— *al*, albumen, proprement dit; *ca*, cellule apicale et *cb*, cellule basale du proembryon bicellulaire; *cc*, cellule-fille supérieure de la cellule apicale; *cch*, cellule chalazienne isolée lors du premier cloisonne-ment de l'albumen; *cd*, cellule-fille inférieure de la cellule apicale; *ci*, cellule inférieure de la tétrade proembryonnaire; *cm*, cellule micro-pylaire isolée lors du premier cloisonnement de l'albumen; *cot*, cellule-mère du cotylédon; *d*, cel-lule-fille supérieure de *m*; *de*, dermatogène; *f*, cel-lule-fille inférieure de *m*; *h*, hypophyse; *hc*, haus-torium chalazien provenant de l'albumen; *hm*, haustorium micropylaire provenant de l'albumen; *iec*, initiales de l'écorce de la racine; *m*, cellule intermédiaire de la tétrade proembryonnaire; *n*, cellule-fille supérieure de *ci*; *n'* cellule-fille inférieure de *ci*; *oi*, octants inférieurs; *os*, octants supérieurs; *pe*, périblème; *pl*, plérome; *q*, qua-drants; *sy*, synergides.
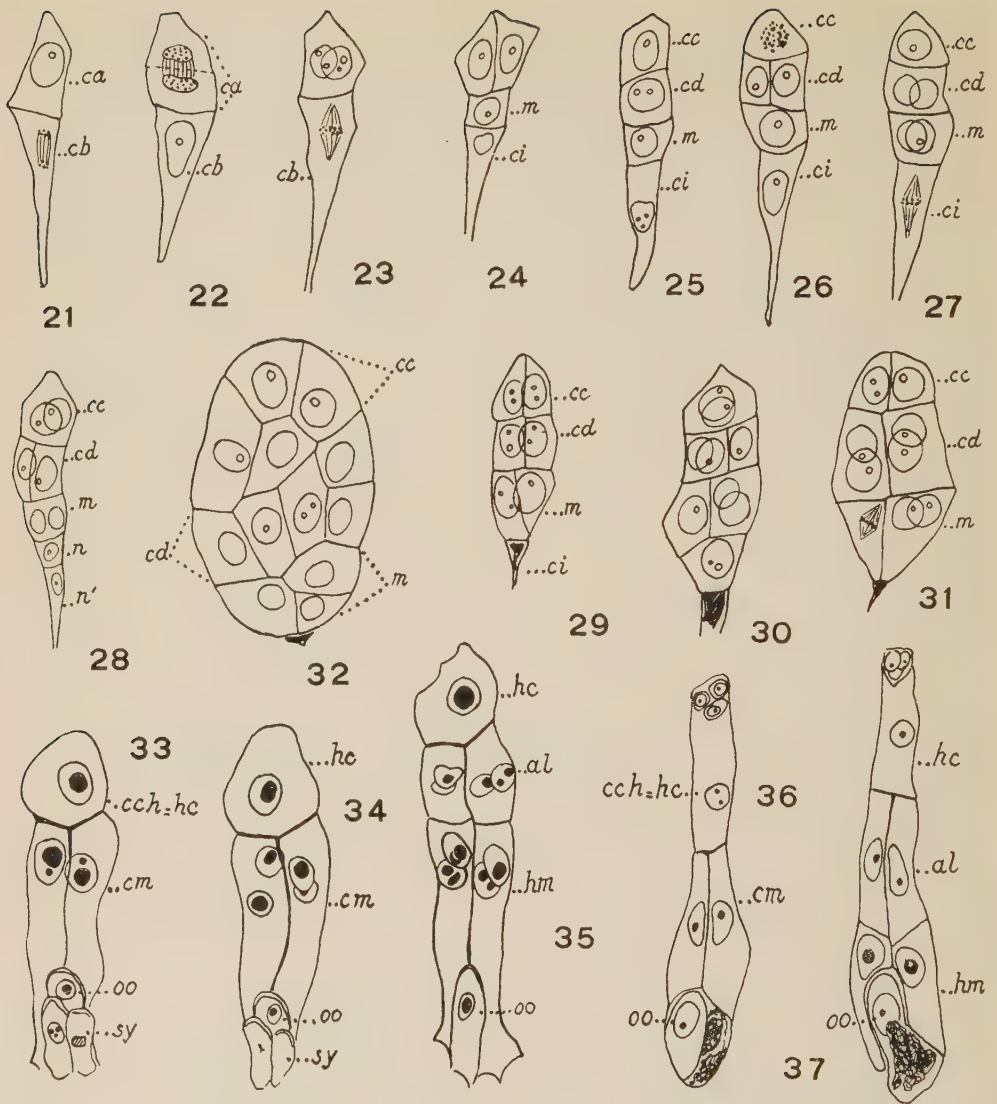
FIGS. 21-37 — Figs. 21-32. Embryogénie de l'*Aeginetia indica* Linn. Fig. 25. Tétrade en C_2; c'est à des tétrades de cette catégorie que se rattachent généralement les diverses formes proembryonnaires. Figs. 23, 24. Tétrades en A_2. (D'après Tiagi. 1952b; les figures ont été légèrement schématisées; leur orientation à été modifiée; les lettres ont été ajoutées.) Figs. 33-35. Les premiers stades du développement de l'albumen chez l'*Alonsoa caulauliata* Ruiz. et Pav. — Ils se rattachent au type *Verbascum*, simplifié au niveau de l'haustorium chalazien; les initiales de l'albumen proprement dit et de l'haustorium micropylaire sont groupées en étages quadricellulaires: c'est à la troisième génération qu'elles se différencient à partir de la cellule micropylaire. (D'après Crété, 1950c.) Figs. 36, 37. Les premiers stades du développement de l'albumen chez l'*Aeginetia indica* Linn. — Ils se rattachent au type *Veronica* par le groupement, en étages bicellulaires, des initiales de l'albumen proprement dit et de l'haustorium micropylaire: ces initiales se différencient à partir de la cellule micropylaire dès la deuxième génération. (D'après Tiagi, 1952g) les figures ont été légèrement schématisées; leur orientation a été modifiée; les lettres ont été ajoutées.)

de tenir compte, définitivement, de ces observations pour un certain nombre de raisons: d'abord, les dimensions du noyau de la cellule basale, *cb*, du proembryon bicellulaire sont étonnamment faibles, comparées à celles qu'atteint le noyau dont il est issu, comparées également à ce qu'elles sont dans la noyau de la cellule apicale *ca*, soeur de *cb* (Figs. 13-15). Il est regrettable que Kadry n'ait pas vu de mitoses dans les oospores ou n'ait pas figuré les noyaux issus de ces cinèses immédiatement après leur séparation, quand ils ont encore un volume comparable. Ensuite, Kadry explique que la cellule *cc* se divise transversalement en deux éléments qu'il appelle *c* et *m*; aucun dessin ne vient à l'appui de cette affirmation et le passage de la Fig. 16 à la Fig. 17 peut aussi bien se faire par division longitudinale de *cc* et transversale de *m*. Enfin, les descriptions qui correspondent aux stades ultérieurs du développement (Figs. 19, 20) ne tiennent pas compte du nombre des noyaux au niveau de chacun des étages et sont par suite absolument insuffisantes pour permettre l'établissement des lois qui président au développement de l'embryon. Aussi, les observations de Kadry, à ce sujet, doivent être, à la fois, complétées et contrôlées par de nouvelles recherches portant sur la même espèce. On sait en effet, grâce à Tiagi, que, dans une espèce voisine, le *Cistanche tubulosa*, l'embryogenèse se rattache au type habituel des Crucifères.

Kadry a comparé les segmentations de l'embryon, chez le *Cistanche tinctoria*, à celles que Juliano (1935) a décrites chez l'*Aeginetia indica* et Worsdell (1897), chez le *Christisonia subacaulis*. Johansen (1950) rapporte ces espèces au type "Caryophyllad", ce qui correspond à la seconde période du système de Souèges. Malheureusement, le botaniste égyptien n'a pas su que Tiagi avait révélé, en 1952b, l'inexactitude des descriptions de Juliano; quant aux dessins de Worsdell, ils sont trop imprécis pour permettre l'identification d'un type embryonomique.

D'autres embryologistes ont eu l'occasion de décrire ou de dessiner l'un ou l'autre des stades de l'embryogenèse chez des Orobanchacées; il s'agit tout particulièrement de Cooke & Schively (1904), de Persidsky (1926), de Cassera (1935), de Srivastava (1939).

B. Scrofulariacées

Souèges a établi le premier les lois qui président au développement de l'embryon chez les Scrofulariacées. Chez le *Veronica arvensis* L. (1921), comme chez le *Verbascum blattaria* L. (1935), elles répondent au type embryonomique du *Capsella bursa-pastoris*, appelé couramment type des Crucifères, et qui dérive du type fondamental du *Myosurus minimus* (Souèges, 1948). C'est également le cas, par exemple, pour le *Chaenostoma foetidum* (Jacq.) Benth. (Crété, 1948), le *Nemesia melissaefolia* Benth. et le *Nemesia floribunda* Lehm. (Crété, 1950b), pour l'*Alonsoa caulauliata* Ruiz. et Pav. (Crété, 1950c; 1950d), le *Digitalis purpurea* L. (Crété, 1953) l'*Erinus alpinus* L. (Crété, 1954a). Le développement de l'embryon obéit donc à des lois identiques chez les Scrofulariacées et les Orobanchacées. Dans les deux cas, l'hypophyse provient de la cellule *d*, fille supérieure de *m*; mais les premières cloisons, au niveau des octants supérieurs semblent être toujours périclines chez les Scrofulariacées, alors qu'elles sont diversement orientées chez les Orobanchacées.

C. Gesnériacées

Hielscher (1883), à propos du *Streptocarpus polyanthus*, Glišic (1924), lors de son étude sur les *Ramondia*, ont donné les premières indications sur l'embryogénie des Gesnériacées. Glišic, en particulier, a conclu que les divisions cellulaires de l'embryon concordaient assez exactement avec celles du *Capsella*. C'est effectivement encore au type du *Capsella bursa-pastoris* que se rapporte le développement de l'embryon chez les Gesnériacées (Crété, 1942; Thathachar, 1942, 1943). Aussi bien chez un hydride du genre *Streptocarpus* que chez le *Ramondia pyrenaica* Rich. (Crété, 1942), les anomalies des premiers cloisonnements au niveau des octants rapprochent tout particulièrement les Gesnériacées et les Orobanchacées et pourraient contribuer à faire considérer ces deux familles comme appartenant à un type relativement primitif.

D. Bignoniacées

C'est Souèges (1940) qui a, le premier, défini les lois qui président au développement du jeune sporophyte chez une Bignoniacée, le *Catalpa kaempferi* Sieb. & Zucc. (Figs. 38-59) " L'embryon du *C. kaempferi*, a-t-il écrit, peut être très étroitement comparé à celui du *Veronica arvensis*, les données embryogéniques justifiant ainsi pleinement les rapports déjà établis entre les Bignoniacées et les Scrofulariacées. Les deux espèces se rattachent au type embryonomique des Crucifères. On observe cependant, chez le *Catalpa*, des caractères différentiels assez importants qu'il importe de bien dégager ". En effet, la tétrade appartient normalement à la série A_2 (Fig. 40), ce qui justifie la classification de l'embryon dans le premier groupe de la première période embryogénique, mais il arrive aussi (Figs. 47, 48) qu'elle appartienne à la série C_2, c'est à dire qu'elle soit linéaire et filamenteuse; compte-tenu du mode de division ultérieur des éléments supérieurs cc et cd de la tétrade, ces formes viennent se ranger dans le troisième groupe de la même période. En plus de ces variations au niveau des tétrades, le proembryon présente encore une autre particularité: les quatre quadrants, au lieu de se situer dans un plan horizontal, comme chez le *Capsella* et les Scrofulariacées, se disposent dans un plan vertical, comme chez les Solanacées, même lorsqu'ils proviennent d'une tétrade en A_2 (Figs. 41-45). Enfin, les deux quadrants supérieurs peuvent eux-mêmes se segmenter transversalement en deux étages superposés de deux blastomères (Fig. 46), au lieu de se diviser verticalement pour donner quatre octants supérieurs, typiquement disposés dans un même plan autour de l'axe. Quand les octants sont normalement groupés en un étage quadricellulaire, les premières parois, à leur niveau, peuvent être tantôt périclines (Figs. 50-52 à g.), séparant d'emblée le dermatogène, tantôt anticlines à direction horizontale (Fig. 51 à d.) ou verticale (Figs. 50, 52 à d.).

FIGS. 38-58 — Embryogénie du *Catalpa kaempferi* Sieb. & Zucc. Fig. 40. Tétrade appartenant à la catégorie A_2; c'est à des tétrades de ce type que se rattachent la plupart des formes proembryonnaires. Fig. 48. Tétrade appartenant à la catégorie C_2; à ce type de tétrade se rattachent les formes figurées en 47, 49. (D'après Souèges, 1940.)

II. Le développement de l'albumen

A. Orobanchacées

Dans tous les cas, une cloison transversale isole une cellule chalazienne et une cellule micropylaire. La cellule chalazienne, caractérisée par son origine et son emplacement, par une perte totale ou presque totale de son pouvoir de division, par sa non-intervention dans l'édification de l'albumen proprement dit et son existence fugace, se comporte comme un haustorium répondant à la définition que j'en ai donnée en 1951 (Crété, 1951). Pour Kadry (1955), un haustorium, pour mériter son nom, doit faire preuve d' '' agressivité '' ou s'accroître en dehors du sac embryonnaire; cette définition correspond étroitement à l'étymologie du terme, mais il n'y a, à mon avis, aucune raison de ne pas conserver aux cellules chalaziennes un peu moins actives, au moins en apparence, la même dénomination; il suffit d'indiquer que l'haustorium exerce ses fonctions avec plus ou moins d'intensité. La cellule chalazienne des Orobanchacées ne se cloisonne généralement pas. Elle demeure même uninucléée chez l'*Aeginetia indica* Linn. (Figs. 36, 37) (Tiagi, 1952b), peut également renfermer un seul noyau hypertrophié chez le *Cistanche tubulosa* Wight. (Tiagi, 1952a). Mais, le plus souvent, elle contient deux noyaux: c'est le cas des *Orobanche hederae* Duby. (Glišić, 1929), *O. teucrii* Schultz (Crété, 1942), *O. uniflora* (Cassera, 1935), *O. aegyptiaca* Pers. (Srivastava, 1939; Tiagi, 1951), *O. cernua* Loeffl. (Tiagi, 1951), *Cistanche tubulosa* Wight. (Tiagi, 1952a) et *Cistanche tinctoria* (Kadry, 1955). Plus rarement le nombre des noyaux s'élève à trois ou quatre, ainsi que Persidsky (1926) le relate chez l'*Orobanche cumana* Wall. et l'*Orobanche ramosa* L. Une paroi transversale peut provoquer la division de l'haustorium en deux cellules qui demeurent uninucléées chez l'*Orobanche cernua*, deviennent binucléées chez l'*Orobanche aegyptiaca* (Tiagi, 1951).

La cellule micropylaire, isolée lors du premier cloisonnement de l'albumen, se segmente longitudinalement, en général, Une cloison transversale, différenciée sensiblement à un même niveau dans chacune des cellules-filles, isole les deux initiales de l'albumen proprement dit et deux éléments qui sont à l'origine de l'haustorium micropylaire (Figs. 36 et 37). Les initiales de l'albumen proprement dit se divisent d'abord transversalement. L' haustorium micropylaire demeure bicellulaire et les cellules renferment généralement un seul noyau hypertrophié; elles en ont deux cependant chez le *Lathraea Squamaria* L. (Glišić, 1931-32), l'*Orobanche aegyptiaca* et le *Cistanche tubulosa*. Cet haustorium, particulièrement actif, émet, de façon très générale, d'importants diverticules, à l'intérieur du tégument séminal. On a rapporté qu'il se faisait, dans certains cas, un cloisonnement tout d'abord transversal de la cellule micropylaire, isolée au début de la formation de l'albumen (Cassera, 1935; Srivastava, 1939). Glišić (1929), Tiagi (1952) et Kadry (1955) ont mis en doute l'exactitude de telles observations.

B. Scrofulariacées

Une bibliographie de la question a paru dernièrement (Crété, 1951), mais il y a lieu de la compléter par addition des travaux de Yamazaki sur les *Dopatrium*, les *Deinostema* et les *Gratiola* (1953), sur les *Lindernia*, les *Vandellia* et les *Torenia* (1955), de Crété sur les *Teedia* (1952a), les *Digitalis* (1953), les *Erinus* (1954a), les *Tetranema* (1954b).

Chez les Scrofulariacées, hormis les *Nemesia* (Crété, 1950a; 1950b), le premier cloisonnement de l'albumen, toujours transversal, isole une cellule chalazienne, qui est à l'origine d'un haustorium. Cette cellule peut, ou demeurer unicellulaire et renfermer un (Figs. 33-35) ou deux noyaux, ou donner naissance à deux ou quatre cellules uninucléées, séparées par des parois qui sont disposées longitudinalement. Chez les *Gratiola* toutefois (Glišić, 1933; Yamazaki, 1953), les parois sont horizontales.

Dans la cellule micropylaire provenant également de la première division de l'albumen, la première cloison, presque constamment verticale, isole deux éléments juxtaposés (Fig. 33) qui se segmentent de la même façon (Fig. 34). Les quatre cellules-filles se divisent horizontalement à un même niveau et il se

forme ainsi deux étages quadricellulaires (Fig. 35). L'un de ces étages donne naissance à l'albumen proprement dit, l'autre à l'haustorium micropylaire dont l'activité est généralement plus grande et plus durable que celle de l'haustorium chalazien. Ce type, extrêmement répandu chez les Scrofulariacées, admet, comme chef de file, les *Verbascum* (Glišić, 1936-1937).

Chez les *Veronica*, par contre, la division longitudinale de la cellule micropylaire est suivie du cloisonnement transversal des deux cellules-filles et les initiales de l'albumen proprement dit et de l'haustorium micropylaire comprennent deux éléments seulement, alors qu'elles sont au nombre de quatre dans les albumens qui se rattachent au type des *Verbascum* (Gscheidle, 1924; Weiss, 1932; Glišić, 1936-37). Chez les *Alectorolophus*, le comportement de la cellule micropylaire est identique à celui des *Veronica*; l'haustorium chalazien est unicellulaire et binucléé, l'haustorium micropylaire est formé de deux cellules binucléées (Schmid, 1906).

Le *Gratiola officinalis* L., étudié par Glišić (1933), se différencie nettement des *Veronica* par la division transversale des initiales de l'haustorium micropylaire et de leurs cellules-filles, mais, chez le *Gratiola japonica*, Yamazaki (1953) a constaté que l'haustorium demeurait bicellulaire, que les autres éléments à caractère haustorial provenaient de la différenciation de certaines des cellules de l'albumen proprement dit. Quant à l'haustorium chalazien, il est souvent formé, chez les *Gratiola*, de deux ou trois étages de deux cellules provenant du cloisonnement de la cellule chalazienne isolée au début de la formation de l'albumen.

Dans le type *Pedicularis*, enfin, le cloisonnement de la cellule micropylaire est transversal et donne naissance directement à l'initiale de l'albumen proprement dit dont la première division est verticale et à l'initiale de l'haustorium micropylaire qui se transforme en une vaste cellule tétranucléée. La formation de l'albumen chez de nombreux *Pedicularis*, *Melampyrum* et *Euphrasia*, ainsi que chez le *Tozzia alpina* serait conforme, selon Schmid (1906), au type qui vient d'être décrit. Le fait a été vérifié par Wurdinger (1910) chez *l'Euphrasia rostkoviana*; certains espèces de *Veronica* présenteraient également le même comportement (Weiss, 1932). Ce sont donc surtout des espèces appartenant aux Rhinanthoïdées parasites qui se rapporteraient au type *Pedicularis*.

C. GESNÉRIACÉES

Le développement de l'albumen chez les Gesnériacées est absolument comparable à ce qu'il est chez les Scrofulariacées. Dans tous les cas, sauf peut-être chez les *Streptocarpus* (Crété, 1942), le premier cloisonnement de l'albumen isole une cellule chalazienne qui est à l'origine d'un haustorium. Cette cellule-mère ne se divise pas et demeure uninucléée chez le *Ramondia nathaliae* (Glišić, 1924), le *Klugia zeylanica* (Schnarf, 1921), le *Ramondia pyrenaica* Rich. (Crété, 1942), le *Rhyncoglossum obliquum* Bl. (Thathachar, 1943); elle devient binucléée chez le *Corytholoma cyclophyllum* (Laurent, 1923) le *Didymocarpus tomentosa* Nt. (Thathachar, 1942), les *Roettlera* (Glišić, 1934), l'*Alloplectus sanguineus* Mart. (Crété, 1955), le *Chirita lavandulacea* Stapf. (Crété, 1949); la cellule-mère se divise longitudinalement en deux éléments uninucléés chez certaines formes de l'*Haberlea rhodopensis*, dont d'autres formes présentent, par contre, des haustoriums à trois cellules, ou réduits à une cellule binucléée (Glišić, 1928), ce qui fait que cette espèce fournit un exemple excellent de l'évolution qui peut se produire dans un appareil haustorial.

La cellule micropylaire, sœur de la cellule chalazienne dont les destinées viennent d'être étudiées, se divise presque toujours à l'aide d'une cloison longitudinale. Les deux cellules-filles prennent chacune une paroi transversale et il se constitue, de la sorte, deux étages bicellulaires. L'un des étages est à l'origine de l'albumen proprement dit, l'autre donne naissance à l'haustorium micropylaire, qui peut demeurer bicellulaire (*Corytholoma*, *Didymocarpus*, *Chirita*, *Rhynchoglossum*) ou devenir unicellulaire par résorption de la cloison longitudinale

(*Roettlera*); chez l'*Alloplectus sangui-
neus*, il présenterait le même comporte-
ment que chez les *Roettlera*, mais on as-
siste, en plus, à la fragmentation ul-
térieure des deux noyaux. Chez cer-
taines formes de l'*Haberlea rhodopensis*,
chez le *Ramondia pyrenaica*, il devient
quadricellulaire par cloisonnement trans-
versal des deux éléments initiaux.

Dans un type bien différent du dé-
veloppement de l'albumen, le cloisonne-
ment de la cellule micropylaire, issue de la
première division de l'albumen, est non
plus longitudinal, mais transversal et
isole d'emblée une initiale de l'albumen
proprement dit et une initiale de l'haus-
torium micropylaire. L'haustorium de-
vient ensuite bicellulaire par cloisonne-
ment longitudinal (*Klugia*) ou quadri-
cellulaire par division transversale des
cellules-filles de l'initiale (*Ramondia na-
thaliae* et *Ramondia serbica*).

D. BIGNONIACÉES

Tout récemment, j'ai émis l'opinion
que les Bignoniacées ne présentaient,
dans l'état actuel de nos connaissances,
que deux types bien définis du développe-
ment de l'albumen, le type *Catalpa* et le
type *Amphicome* (Crété, 1952 b).

Chez l'*Amphicome arguta* (Royle)
Lindl., la cellule chalazienne, isolée lors de
la première division de l'albumen, reste
indivise et conserve un seul noyau. La
cellule-soeur de la cellule chalazienne ou
cellule micropylaire se partage longitu-
dinalement en deux éléments juxtaposés
qui se cloisonnent transversalement. L'un
des étages bicellulaires donne naissance à
l'albumen proprement dit, l'autre à un
haustorium micropylaire qui, probable-
ment, devient unicellulaire et binucléé
par rupture de la paroi médiane qui
séparait primitivement les deux cellules.

Mauritzon (1935) a décrit, mais avec
une précision insuffisante, un type *In-
carvillea*, qui pourrait se révéler, à la
lumière de nouvelles recherches, très
proche du type *Amphicome*, il ne me
paraît pas possible d'en tenir compte
pour le moment.

Par contre, le type *Catalpa*, également
décrit par Mauritzon (1935), est par-
faitement défini. La cellule chalazienne,
provenant du premier cloisonnement de
l'albumen, donne naissance à deux ou
quatre éléments juxtaposés. La cellule-
soeur ou cellule micropylaire est a l'ori-
gine de deux ou, plus souvent, de quatre
éléments séparés par des cloisons longi-
tudinales. Des parois transversales iso-
lent, à partir de ces éléments, les initiales
de l'albumen proprement dit et un groupe
de cellules dirigées vers le micropyle et
dont les destinées sont beaucoup moins
précises. Il n'est pas possible, en tout
cas, d'identifier un haustorium micro-
pylaire à des stades quelque peu avancés
du développement de l'albumen. Au type
Catalpa se rapportent, d'après Mauritzon
(1935), le *Bignonia tveediana*, le *Pithe-
coctenium clematideum*, le *Jacaranda mi-
mosaefolia*. On peut également y rat-
tacher le *Parmentiera cerifera* et le *Tecoma
stans* (Govindu, 1950), le *Bignonia mega-
potamica* Spreng (Swamy, 1941).

Conclusions

Le recours aux critères tirés du déve-
loppement de l'albumen et de l'embryon
confirme avant tout l'existence de rela-
tions étroites entre les Orobanchacées et
les Gesnériacées. Dans les deux familles,
les segmentations qui assurent l'édifica-
tion de l'albumen sont absolument com-
parables. Elles ont pour effet d'isoler,
dès le premier cloisonnement, une cellule-
mère d'un haustorium chalazien et une
cellule micropylaire qui, après deux séries
de segmentations, donne naissance à
deux étages de deux initiales, correspon-
dant, les unes à l'albumen proprement dit,
les autres à l'haustorium micropylaire.
Les seules variations importantes de struc-
ture intéressent les haustoriums; elles se
retrouvent, identiques, dans l'une et
l'autre famille. Si les observations de
Cassera (1935) et de Srivastava (1939),
concernant un cloisonnement transversal
de la cellulle micropylaire chez certains
Orobanche, sont, finalement, bien fondées,
on retrouve des faits semblables chez les
Klugia et quelques espèces du genre
Ramondia, parmi les Gesnériacées. Dans
les deux familles, le proembryon se rat-
tache au type fondamental du *Capsella
bursa-pastoris*, l'hypophyse provient de
la cellule *d*, fille supérieure de la cellule

intermédiaire *m* de la tétrade, la formation du dermatogène est souvent retardée, au niveau des octants supérieurs, par la production initiale de cloisons anticlines, verticales ou horizontales.

Du point de vue de leur embryologie, les Orobanchacées et les Gesnériacées pourraient être, sans, inconvénient, confondues en une famille unique, mais elles n'ont pas d'affinités aussi étroites avec les Scrofulariacées, où le développement de l'albumen présente, nous l'avons vu, d'importantes variations. Dans la majeure partie des genres étudiés jusqu'ici, il se rattache à un type *Verbascum*, caractérisé par le groupement en étages quadricellulaires des initiales de l'haustorium micropylaire et de l'albumen proprement dit. A partir de la cellule micropylaire, différenciée lors du premier cloisonnement de l'albumen, ces initiales s'individualisent seulement à la troisième génération. Le type *Verbascum* de développement de l'albumen n'a jamais encore été rencontré chez les Orobanchacées et les Gesnériacées. Un nombre moins important de Scrofulariacées, se caractérisant par une structure florale assez particulière, comme les *Gratiola* et les *Veronica*, ou par un parasitisme plus ou moins poussé comme les *Alectorolophus* et quelques genres voisins, possèdent des albumens identiques, par leur structure et leur origine, à ceux des deux autres familles. Les initiales sont groupées en étages bicellulaires et leur différenciation à partir de la cellule micropylaire se fait dès la deuxième génération. Les modifications, qui se produisent dans le nombre définitif des cellules au niveau des formations haustoriales, s'observent également chez les Orobanchacées et les Gesnériacées. Enfin, le développement du tissu de réserve séminal peut également se rapporter, chez les Scrofulariacées, à un type *Pedicularis*, caractérisé par une individualisation encore plus précoce des initiales de l'albumen proprement dit et de l'haustorium micropylaire; à ce type se rattachent le *Roettlera*, le *Ramondia nathaliae*, le *Ramondia serbica* chez les Gesnériacées, et, de plus, les cas anormaux signalés par Cassera et Srivastava chez les Orobanchacées. Il est bien évident que l'embryologie des Scrofulariacées nous est encore insuffisamment connue et qu'il faudra nous adresser à un bien plus grand nombre de genres et d'espèces, si nous voulons nous assurer approximativement de la répartition des différents types d'albumens dans la famille. A cette condition seulement, il nous sera possible de procéder à un remaniement complet de la classification de cet important groupement, d'y créer, en particulier, de nouvelles subdivisions, dont il sera relativement facile de déterminer les relations qu'elles présentent avec les autres familles de Gamopétales. Chez les Scrofulariacées, comme dans les Orobanchacées et les Gesnériacées, l'embryon se rattache au type fondamental du *Capsella*, l'hypophyse prend naissance à partir de la cellule *d*, fille de *m*, mais il semble bien que les premiers éléments du dermatogène se séparent toujours d'emblée, au niveau des octants supérieurs, au moyen de parois périclines. Cette particularité, assurément secondaire, s'oppose pour le moment à un rapprochement trop étroit des Scrofulariacées et des deux autres familles; nous manquons malheureusement, à ma connaissance, de données précises sur le comportement, à ce stade, des Rhinanthoïdées parasites que leur mode de vie et leur embryologie apparenteraient tout particulièrement aux Orobanchacées.

Par rapport aux trois familles précédentes, les Bignoniacées présentent d'importantes particularités. D'abord, les albumens du type *Catalpa*, en dépit de l'absence d'un haustorium micropylaire, se rapprocheraient plutôt, chez les Scrofulariacées, des albumens du type *Verbascum*. Seuls, les albumens du type *Amphicome* sont tout à fait comparables à ceux des Orobanchacées, des Gesnériacées et de certains *Veronica*. Le développement embryonnaire fait preuve, à son tour, d'une réelle originalité par la disposition des cellules quadrants et octants et, surtout, par la présence, à côté de tétrades en T de la catégorie A$_2$, de tétrades linéaires de la catégorie C$_2$. Tiagi, pour sa part, a découvert également la coexistence des deux types de tétrades chez une Orobanchacée, l'*Aeginetia indica*. Chez les Orobanchacées, où l'embryogénie de nombreux repré

sentants de la famille nous est actuellement connue, il est permis de penser que le cas de l'*Aeginetia* est assez exceptionnel. Celui du *Catalpa kaempferi*, chez les Bignoniacées, mérite évidemment d'être signalé tout particulièrement, mais il est imprudent d'en vouloir tirer présentement trop de conclusions, puisque c'est le seul exemple que nous ayons encore de l'embryogenèse dans la famille. Dès maintenant, nous pouvons dire des Bignoniacées qu'elles ne constituent pas une famille homogène, puisque le développement de leur albumen répond au moins à deux types bien différents. D'autre part, l'unique exemple connu de leur embryogenèse contribue à accentuer les divergences entre ce groupement d'une part, les Scrofulariacées et les Gesnériacées d'autre part.

J'ai volontairement limité cette étude aux quelques familles que Fritsch, dans la classification d'Engler & Prantl, considère comme particulièrement voisines les unes des autres. Il est bon de rappeler que, dans la sous-série des Solaninées, seules les Solanacées, parmi les familles dont l'embryogenèse a été étudiée sur un ou plusieurs représentants, répondent à un type embryonomique différent de celui du *Capsella bursa-pastoris*, que dans toutes les familles, à l'exception des Solanacées et des Nolanacées, il existe des albumens à formations haustoriales typiques et que nous pourrions, avec intérêt, leur appliquer les critères embryologiques en vue de résoudre les nombreux problèmes que pose leur classification. Ce qui rend actuellement ce travail fort difficultueux, c'est l'insuffisance en nombre des données embryologiques et les contradictions que révèlent trop souvent celles dont nous disposons.

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THE STRUCTURE AND DEHISCENCE OF THE ANTHER IN *MEMECYLON* AND *MOURIRIA*

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Memecylon and *Mouriria* belong to the small subfamily Memecyloideae of the Melastomaceae. While the majority of members of the Melastomaceae show a typical poricidal dehiscence of their anthers, those belonging to the subfamilies Memecyloideae and Astronioideae are exceptional in having the usual longitudinal dehiscence. After investigating the morphology and structure of the poricidal anthers of about 11 genera and 18 species of the subfamily Melastomoideae, Zeigler (1925) felt that in the Memecyloideae and Astronioideae, which are supposed to show kinship with the Myrtaceae and Lythraceae, there probably occur transitions from the typical longitudinal dehiscence to the poricidal dehiscence and from a typical fibrous endothecium to the reduced type of endothecium found in poricidal anthers. In his revision of the genus *Mouriria*, Morley (1953) described the gross features of the stamens in several species. He found that the extent of splitting of the anther wall, during dehiscence, varies in the different sections of this genus.

In the present instance, the structural peculiarities of the anther of *Memecylon* and *Mouriria* have been investigated with a view to elucidate the mechanism of dehiscence.

Materials and Methods

Flowers of *Memecylon edule* Roxb., *M. heyneanum* Benth. and *Mouriria guianensis* Aubl. were fixed in formalin-acetic-alcohol. *M. heyneanum* was collected from Lal Bagh, Bangalore; and the others were obtained from the Indian Botanic Gardens, Calcutta. Gross features of the anthers were observed from material mounted in lactophenol. The anatomical studies were made from microtome sections, 8-12 µ thick, of material dehydrated and imbedded in paraffin in the usual way. Heidenhain's iron-haematoxylin, followed by eosin in clove oil, was used for staining.

Observations

Memecylon — There are eight stamens arising from the shallow cup-like floral tube. The four antepetalous stamens arise from a higher level than the antesepalous ones.

As in other Melastomaceae, the stamen filament is inflexed in bud and straightens out as the flower opens. The two thecae are curved. The massive connective bears
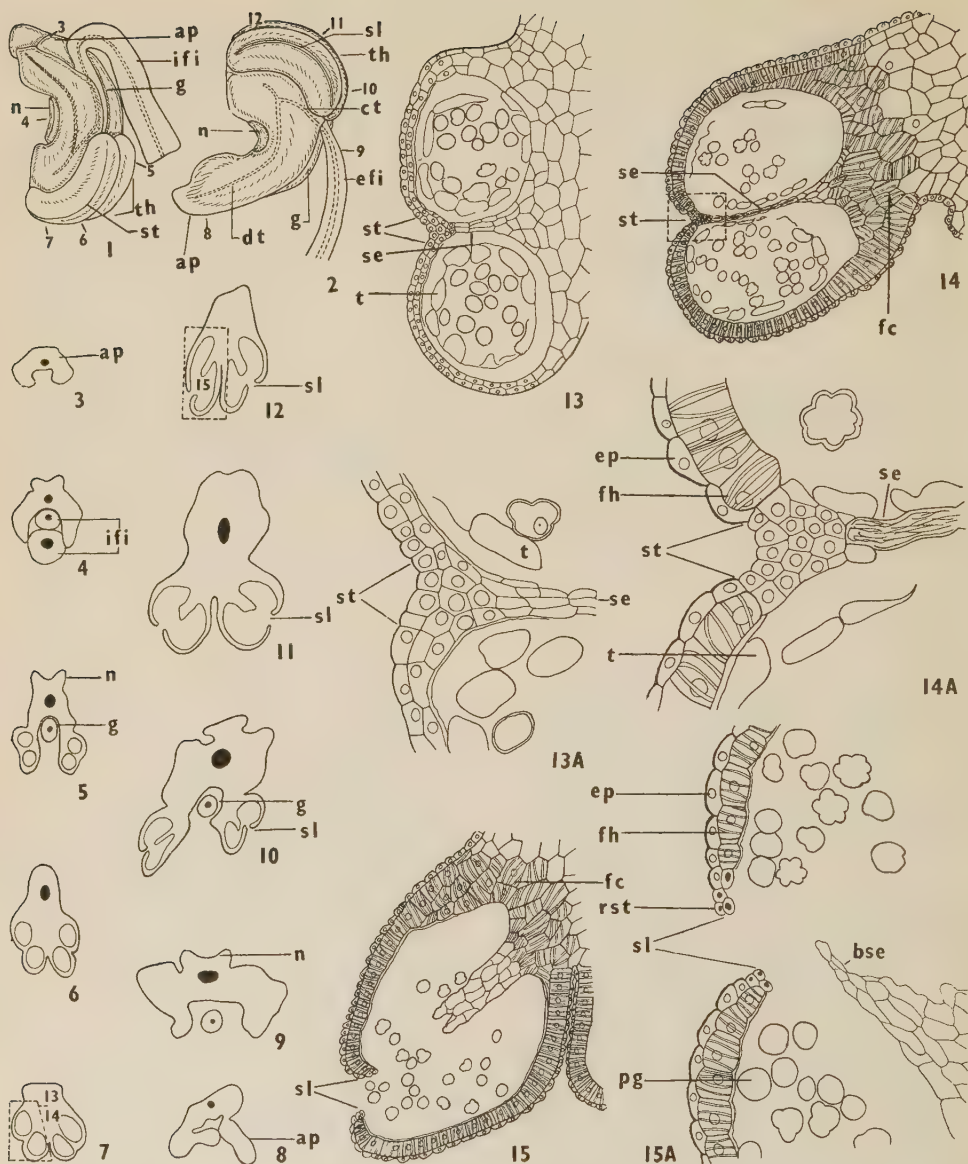
FIGS. 1-15A — *Memecylon* (*ap*, appendage; *bse*, broken septum; *ct*, connective vascular trace; *dt*, dorsal appendage trace; *efi*, erect filament; *ep*, epidermis; *fc*, fibrous part of the connective; *fh*, fibrous hypodermis; *g*, groove, *ifi*, inflexed filament; *n*, nectary; *pg*, pollen grains, *rst*, remains of stomial tissue; *se*, septum; *sl*, slit; *st*, stomium; *t*, tapetum; *th*, thecae). Fig. 1. Young inflexed stamen. × 20. Fig. 2. Part of erect stamen. × 20. Figs. 3-7. T.s. young anther at levels indicated in Fig. 1. × 32. Figs. 8-12. T.s. dehisced anther at levels indicated in Fig. 2. × 32. Fig. 13. T.s. part of young anther. × 232. Fig. 13A. Part of above magnified. × 607. Fig. 14. T.s. part of older anther. × 143. Fig. 14A. Part of above magnified. × 607. Fig. 15. Part of t.s. dehisced anther. × 143. Fig. 15A. Magnified view of a part of a dehisced anther in t.s. × 320.

a large nectar disc on its back and is produced basally into a curved horn-like dorsal appendage (Figs. 1, 2). The filament is fixed below the thecae in a groove that runs on the ventral side of the horn.

The vascular bundle of the filament continues into the connective (Fig. 2, *ct*) giving off a long dorsal descending trace (*dt*) which runs along the greater length of the appendage. The appendage consists of a homogeneous tissue. Sphaeraphides occur in a few cells of the connective. Figs. 3-7 are transections of an inflexed and undehisced stamen and Figs. 8-12 of an erect and dehisced anther. The figures show the limits of the thecae, appendage, the groove (g) enclosing the filament (*ifi*), the nectar disc and the vasculation. It will be seen that the dehiscence of the anther is complete and slits are formed along the entire length of the two thecae.

Figs. 13, 13A are magnified views of parts of young anthers in which the stomia are not yet differentiated and the epidermal and hypodermal cells along the septum look alike. But Figs. 14, 14A, which are of an older anther, show the anther wall and the stomia region fully differentiated. The hypodermis has developed into a typical fibrous layer of large, radially enlarged cells with banded thickenings. The general epidermal cells (*ep*) have become laterally stretched. Each stomium is situated in a lateral furrow; the epidermal, hypodermal and other cells, of which it is composed, are thin-walled. The general epidermis and the fibrous hypodermis are, therefore, interrupted by the unthickened stomial area. Besides the general hypodermal layer, several cells of the connective also acquire the fibrous thickenings. The stomia develop along the entire length of the thecae and so does the fibrous hypodermal layer.

As the anther matures, there is a gradual stretching of the septa which eventually break down beneath the stomia. This causes the fusion of the adjacent pollen sacs of each anther theca (Figs. 10-12). Due to the tension set up by the shrinking fibrous hypodermis, the anther wall first folds and then ruptures in the stomial

region. The split edges of the wall curve inwards and away from each other to form a complete longitudinal slit for the escape of the pollen (Figs. 15, 15A).

Mouriria — The flower of *Mouriria guianensis* is pentamerous. The five antepetalous stamens are taller than the five antesepalous ones.

Externally the stamens are similar to those of *Memecylon*. The anther bears a discoid nectary and a dorsal horn-like appendage (Figs. 16, 17). The appendage receives a dorsal branch of the connective vascular bundle and a weaker trace branches off for the nectary (Fig. 18). In the matter of its structural details, however, as well as in the mode of dehiscence the anther differs considerably from that of *Memecylon*.

The ventral pollen sac of each theca is slightly longer and its bent tip is arched over that of the shorter dorsal pollen sac (Fig. 18). Dehiscence is incomplete and occurs by short slits confined to the upper part of the curved thecae (Fig. 19).

Figs. 20-23 are transections of a young inflexed stamen at the levels indicated in Fig. 18, and Figs. 24-27 are those of an erect dehisced anther at the levels indicated in Fig. 19. Lateral stomial depressions are evident only in the upper part of the anther (Fig. 23). Lower down they become shallower (Fig. 22) and are soon eliminated. Correspondingly, in the dehisced anther the slits are wide above (Fig. 27) and narrow below (Fig. 26). Where stomia do not exist, the anther wall is undehisced and the adjacent pollen sacs remain uncoalesced (Fig. 25).

Figs. 28-31 show the structural details of the dehiscent and indehiscent regions of the anther wall. An epidermis and a heavily sclerified hypodermis constitute the wall of an old anther. Besides, a few cells of the other layers may also become sclerified. In the dehiscent upper part of the anther the cells of the hypodermis are radially elongated (Fig. 28) but towards the middle and base of the anther the hypodermal cells, specially those around the sporangia, are flatter (Fig. 29).
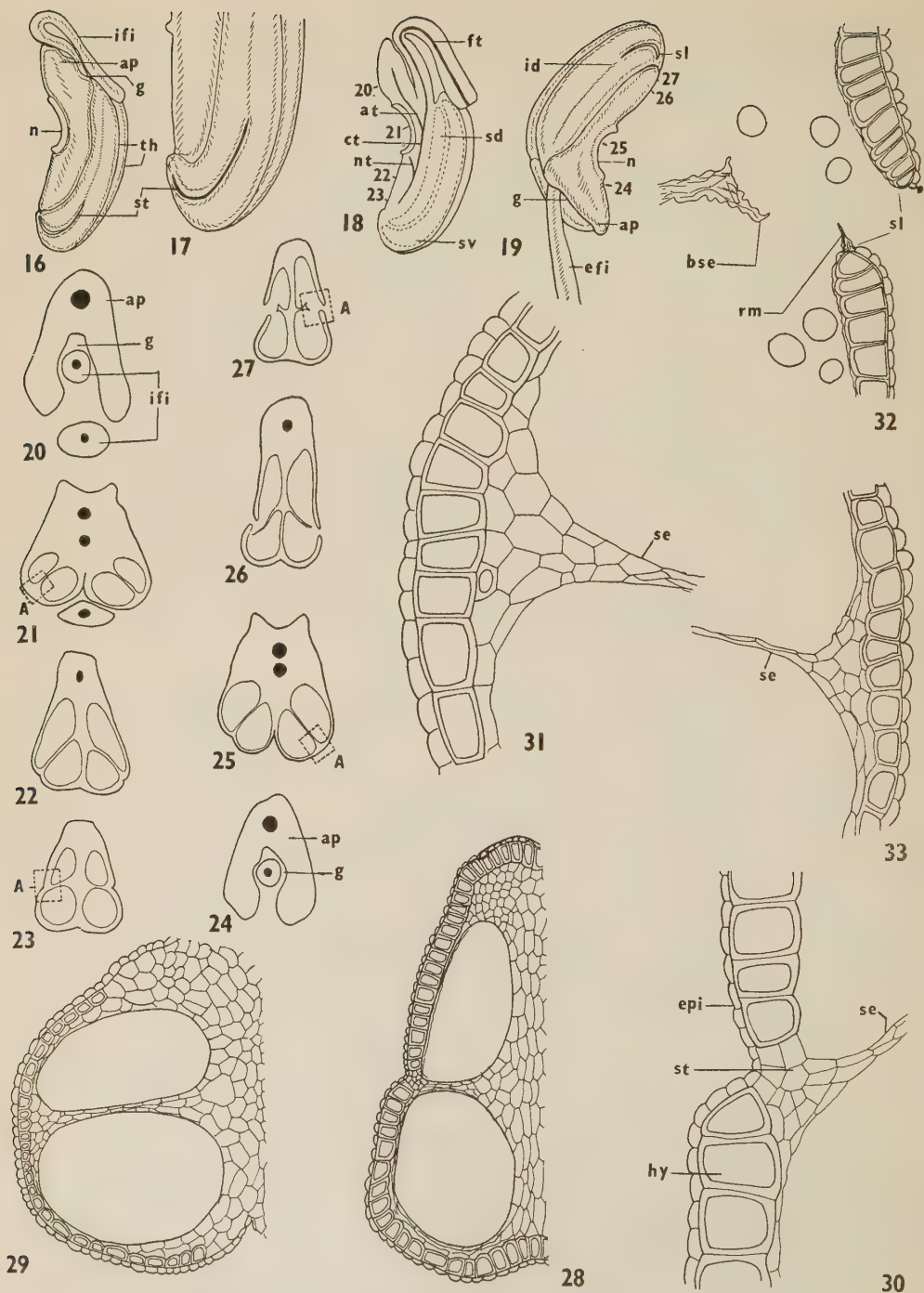
FIGS. 16-33.

In the stomial region the epidermal cells are smaller, the sclerified hypodermis is discontinuous and there is a group of thin-walled cells where the septum meets the anther wall (Fig. 30). Each stomium narrows downward and is soon eliminated altogether. Where stomia are not formed, the sclerified hypodermis and the general epidermis continue uninterrupted across each septum (Fig. 31).

Unlike *Memecylon* there are no fibrous thickenings, but the hypodermis is unequally thickened and serves the mechanical function in dehiscence. The radial and inner tangential walls of its cells are slightly thicker than the outer walls abutting on the epidermis.

As the anther enlarges and matures, the septa between the adjacent pollen sacs become stretched and break down below the stomia along which the anther wall also subsequently splits as a result of the disorganization of the latter. The unequal contraction of the differentially thickened hypodermis causes the broken edges of the anther wall to part widely and allow the escape of pollen through short slits (Fig. 32). The lower part of the anther fails to dehisce due to lack of stomia and the continuity of the thickened layers across the septa (Fig. 33). Moreover, here the septa fail to break so that the pollen sacs remain distinct and uncoalesced in their lower ends.

Discussion

A comparison of the anthers of *Memecylon* and *Mouriria* shows that though morphologically alike, they differ structurally. *Memecylon* shows a longitudinal and complete dehiscence of its anther with associated fibrous hypodermis. The stomia are long and linear and develop along the entire length of the thecae and the fibrous mechanism is also equally well developed all over. Thus, there is absolutely no suggestion of any tendency for restriction of dehiscence. In *Mouriria*, on the other hand, a fibrous layer is wanting and the cells of the hypodermis become differentially thickened. In *M. guianensis*, the form here investigated, the dehiscence is incomplete because of the brevity of the stomia. According to Morley (1953) in the section *Trunciflos* and some species of the section *Acutiflos*, the cells of the sporangial wall are unthickened except a few near the apices of the pollen sacs. The slits of the dehiscent anther extend from half to three-fourths of the length of the pollen sacs and are wider at the apex. In all other sections of the genus the cells of the hypodermal layer showed unequal thickenings of the type described here in *M. guianensis*. Excepting the section *Cyrtotheca*, the slits are further restricted towards the apex. In *Cyrtotheca*, despite such strengthening of the anther wall, dehiscence occurs by slits running the whole length of the pollen sacs. It appears, therefore, that while a strengthening of the anther wall is usually connected with a restriction of the region of splitting, the two features are not always coincident, and as with other features described by Morley, in the matter of dehiscence also *Mouriria* shows an interesting plasticity and diversification.

From what has been described and discussed in the foregoing pages, the conclusion may be reached (*see* also Zeigler, 1925) that some of the Memecyloideae,

like *Mouriria*, show what may be regarded as transitions, from the structure and longitudinal dehiscence typical of angiospermic anthers, to the highly specialized poricidal dehiscence displayed by the majority of the Melastomaceae. Species of *Mouriria* show a strong tendency to restrict the extent of splitting of the anther wall to the distal end, a tendency which points to the evolution of the poricidal mechanism.

Summary

The structural features and dehiscence of the anthers of *Memecylon* and *Mouriria*, two genera belonging to the small subfamily Memecyloideae of the Melastomaceae, are described. While *Memecylon* shows features, which are not very different from those of typical angiospermic anthers, the anthers of *Mouriria* show incomplete stomial development and dehiscence which may be regarded as suggesting a trend towards the specialized poricidal dehiscence seen in the majority of the Melastomaceae included in the subfamily Melastomoideae.

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THE REPRODUCTIVE STRUCTURES OF *PISTACIA CHINENSIS* (ANACARDIACEAE)

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Pistacia chinensis Bunge is a dioecious, deciduous tree with alternate pinnate leaves. It was introduced into California as an ornamental; its chief attraction is the red autumn foliage. Clusters of flower buds of both sexes make their appearance in February or March, in advance of the foliage, in axillary positions on twigs of the previous year. The inconspicuous flowers are fully open in March or April. Pollination is by wind; after this the male flower-clusters fall and the leaves begin to expand. By the end of May, the ovaries of the female flowers form fruits, about 6 mm in diameter. In August or September, the fruits begin to turn red. Many fruits remain empty. This occurs, apparently, by failure of pollination; our cultivated trees are planted in small clusters and show individual variations of a few days in time of anthesis. In October, the fruits which contain developed seeds show themselves ripe by changing colour from red to turquoise blue. They are of no commercial value.

Through the agency of birds, squirrels, and wind, the fruits disappear, almost completely, before the leaves begin to fall.

Material and Methods

Floral buds, flowers, and developing and mature fruits were collected in the public parks of Sacramento at intervals during the years 1954 and 1955. I am indebted to Mr Jerry Olrich, State Gardener, State of California, and to Mr William G. Chorley, Superintendent of Parks, City of Sacramento, who made the material available to me. The material was fixed partly in FAA and partly in Bouin's fluid. The material was dehydrated, imbedded in paraffin, and sectioned in routine fashion. The sections were stained either with safranin and light green or with Heidenhain's haematoxylin.

Observations

INFLORESCENCE — One may find in the literature references to the flower-clusters of the Anacardiaceae as racemes. According to the writer's limited observations, these are inaccurate. The individual flower is borne on a pedicel which stands in the axil of a bract and bears two bractlets. The bractlets may become bracts to further flowers: in other words, bibracteolate pedicels, bearing flowers, may grow in their axils; and the bractlets on these pedicels may become the bracts of further flowers (Fig. 13). Thus the inflorescence is ultimately cymose. In *Pistacia*, cymose clusters as described are borne on a main axis in acropetal succession, forming a thyrse.

THE MALE FLOWER — The male flower (Fig. 1) consists only of stamens, usually 4, 5, or 6, in a whorl at the summit of the pedicel. The vascular supply of this flower (Fig. 2) is simple. It originates as two bundles springing from the stele in the parent axis on the two sides of the bract trace. Entering the pedicel, these two bundles branch to a slight extent; two of the branches, or secondary branches from them, supply the bractlets; the remainder become the single bundles supplying the stamens.

The anthers are quite typical. Each (Fig. 3) consists of a connective, traversed by the stamen bundle, and bearing two lobes, each containing two pollen sacs. At an early stage (Fig. 4) one may recognize an epidermis, several layers of wall cells, and a mass of internal cells. The outermost cells of the internal mass become the tapetum (Fig. 5); the remainder become pollen mother cells. Later (Figs. 10, 12), the wall cells of the outermost layer develop rib-like thickenings while most of the others disappear. The cells of the tapetum become binucleate and are subsequently digested. In the pollen mother cells reduction division occurs in due course. The haploid chromosome number is 15 (Figs. 6, 7). Quadripartition occurs by furrowing. The tetrads are somewhat irregularly tetrahedral (Figs. 8, 9). The mature pollen grains (Fig 11) are spherical, binucleate, with a finely pitted outer wall. The wall may be marked by four vertical grooves in an equatorial whorl; very often, only three or two grooves are present. Contraction of the ribbed hypodermal layer of the anther tears open two clefts, one in each lobe, and releases the pollen grains.

THE FEMALE FLOWER — The female flower (Figs. 14, 15, 16) consists of 4-7 imbricate scale-like perianth segments and a single pistil with dorsiventral symmetry. The ovary is subglobular with one end larger than the other, like an egg laid on a table. A short style bears three spatulate stigmas, the median and largest stigma standing above the large end of the ovary, and the smaller lateral stigmas above the small end. The ventral (inner or upper) surfaces of the stigmas are papillose. The ovary contains a single locule. At the time of flowering this is almost entirely filled by a single basifixed anatropous ovule, symmetrical with regard to the pistil.

It is not possible to distinguish some of the perianth segments as sepals and others as petals. It has not been possible to recognize any consistent phyllotactic pattern in their arrangement. There is no disk. Pistils of different flowers stand in
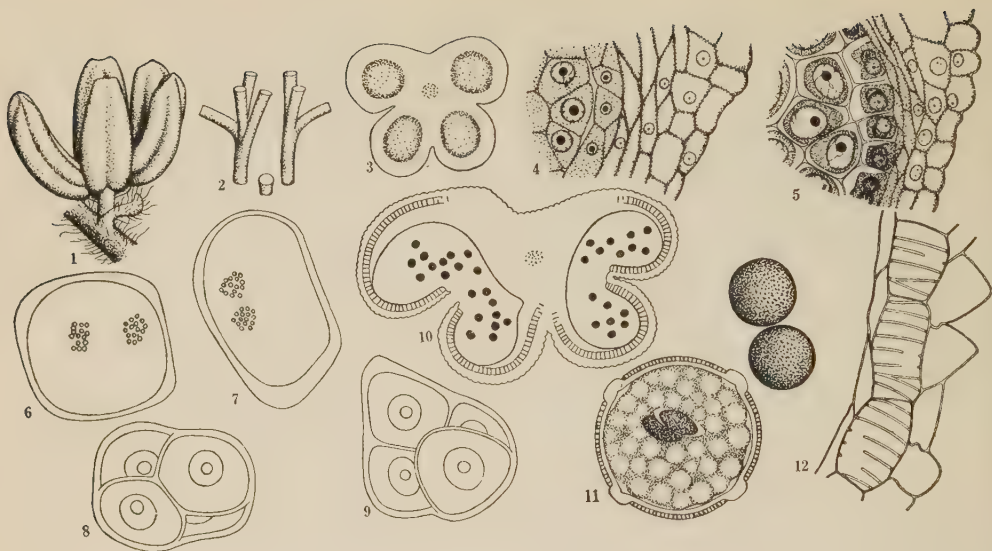
FIGS. 1-12 — Fig. 1. Male flower. × 8.   Fig. 2. Vascular system of male flower. × 40.   Fig. 3. T.s. young anther. × 40.   Fig. 4. Portion of same enlarged. × 320.   Fig. 5. Portion of t.s. older anther. × 320.   Figs. 6, 7. Heterotypic anaphase in pollen mother cells. × 720.   Figs. 8, 9. Microspore tetrads. × 720.   Fig. 10. T.s. mature anther. × 40.   Fig. 11. Binucleate pollen grain. × 720.   Fig. 12. Portion of t.s. mature anther. × 320.

planes which vary at random with respect to the bracts, bractlets, and perianth segments.

The vascular supply of the female flower (Figs. 17, 18) originates like that of the male flower, as two bundles entering the pedicel from the stele of the parent axis on the two sides of the bract trace. The two bundles branch freely and produce a cylinder of several bundles. Two of these, or branches from two of them, supply the bractlets. In the receptacle, the bundles of the single whorl in the pedicel undergo branching and anastomosis to a certain extent and give rise to three concentric whorls of bundles. Those of the outermost whorl are of the same number as the perianth segments and supply them. Those of the middle whorl supply the ovary wall. They branch freely in the lower part of the ovary and become very numerous (Fig. 48). Toward the summit of the ovary, many bundles fuse and many fade out. The median stigma is supplied by three or more bundles. The middle ones come from the sagittal plane of the ovary at

the large end; the lateral ones come from both sides of the sagittal plane of the ovary at the small end. The lateral stigmas are supplied in part by the median bundle at the small end of the ovary, and in part by branches from the same bundles which become the lateral bundles of the main stigma. As to the bundles of the innermost whorl in the receptacle, all of these run together and unite below the insertion of the ovule. The bundle formed by their union traverses the funiculus to the chalaza.

THE OVULE — In the youngest material seen, the locule of the ovary is a dome-shaped cleft. The convex mass of cells within it is the rudiment of the ovule (Figs. 19, 20, from a bud collected early in March. I am sorry to have drawn Figs. 17, 19, 20 and 21 with the median stigma, which may be held to mark the dorsal direction of the gynoecium, to the left. My other lateral views of the gynoecium and its parts are drawn from the other side, with the dorsal direction to the right). A moderately extensive body of hypodermal cells at the mor-

phological apex of the ovule (this is below the mid-point of the dome) undergo periclinal divisions. A certain cell cut off from the dividing layer near its middle is distinctly larger and more darkly staining, and has a larger nucleus than the others. At a slightly later stage (Fig. 21) one finds that the dividing hypodermal cells have produced converging rows. The distinguishable cell formerly seen near the surface lies at the inner end of a row near the middle. It is the megaspore mother cell. Meanwhile, the tissue of the dome which surrounds the dividing hypodermal cells grows forward and produces the rudiment of an integument.

At the time of anthesis (Figs. 22, 30), the ovary and its locule have become considerably enlarged. The basal cells of the ovule have grown to produce a funiculus; this has become elongate and so curved as to form, with the proper ovule carried forward at its free end, nearly a complete circle: the funiculus arises from the floor of the locule, goes up along the large end of the ovary, follows the top of the locule toward the small end, and bears the nucellus with its free end pointing nearly to the base of the funiculus. The integument has grown, but does not extend beyond the nucellus. At the summit of the locule, beneath the base of the style, there is a shallow indentation; an emergence from the upper side of the funiculus projects into this. Another emergence, the obturator, has begun to grow from the base of the funiculus on the side toward the ovule proper. In the chalaza, at the end of the vascular bundle which traverses the funiculus, a few cells have become thick-walled and darkly staining. These are the rudiments of the hypostase. At this stage, pollination and fertilization take place.

THE EMBRYO SAC — At about the time when the stigmas become exposed, the megaspore mother cell cuts off two " cap cells " (Figs. 23, 24, 25). The nuclear divisions involved have not been seen; undoubtedly, they are meiotic. The nucleus of the first cap cell (micropylar diad cell) is a product of the heterotypic division, and divides no further: no tetrad, in the proper sense of the term, is produced. The second cap cell is a non-functional megaspore, and its sister cell is the functional megaspore. Its nucleus divides three times (Figs. 26, 27), producing eight nuclei. An embryo sac of two synergids, an egg, an endosperm mother cell in which two polar nuclei undergo fusion, and three fugitive antipodal cells, is organized (Fig. 28). Thus the embryo sac is of normal Polygonum type. In occasional ovules, abortive megaspore mother cells have been seen. Rarely, both the megaspores produced start developing into embryo sacs (Fig. 29).

POLLEN TUBES: FERTILIZATION — The pollen tubes grow down the middle of the style to the impression on the top of the locule and across the space to the knob on the upper side of the funiculus. They penetrate the vascular bundle in the funiculus and follow this to the chalaza. They are believed not to penetrate the hypostase, but to grow past its margin while it is still of slight extent. Some go straight to the embryo sac and follow its surface to the egg; others go some distance toward the tip of the nucellus and then turn sharply back to the egg. These statements are here illustrated merely by a diagram (Fig. 30): one does not see the entire course of an individual pollen tube, but brief lengths of fine channel.

Fertilization has not been seen. Immediately afterward (Fig. 32) one finds the rather thick-walled tip of the pollen tube projecting into the embryo sac. A small body of darkly staining material at its end is believed to consist of the remnants of one or both synergids. The zygote lies beside or at the end of the tip of the pollen tube. In occasional embryo sacs, one finds a considerable body of cytoplasm with several endosperm nuclei.

DEVELOPMENT OF THE FRUIT — At the time of fertilization, the ovary wall consists, between an outer epidermis and an inner, of ground parenchyma traversed by numerous immature vascular bundles running in the direction of meridians. The majority of these bundles contain one fine schizogenous canal each. At this time, the cells of the inner epidermis begin to divide periclinally (Fig. 31); each one cuts off toward the inside about six cells. At the same time, all the cells of the ovary
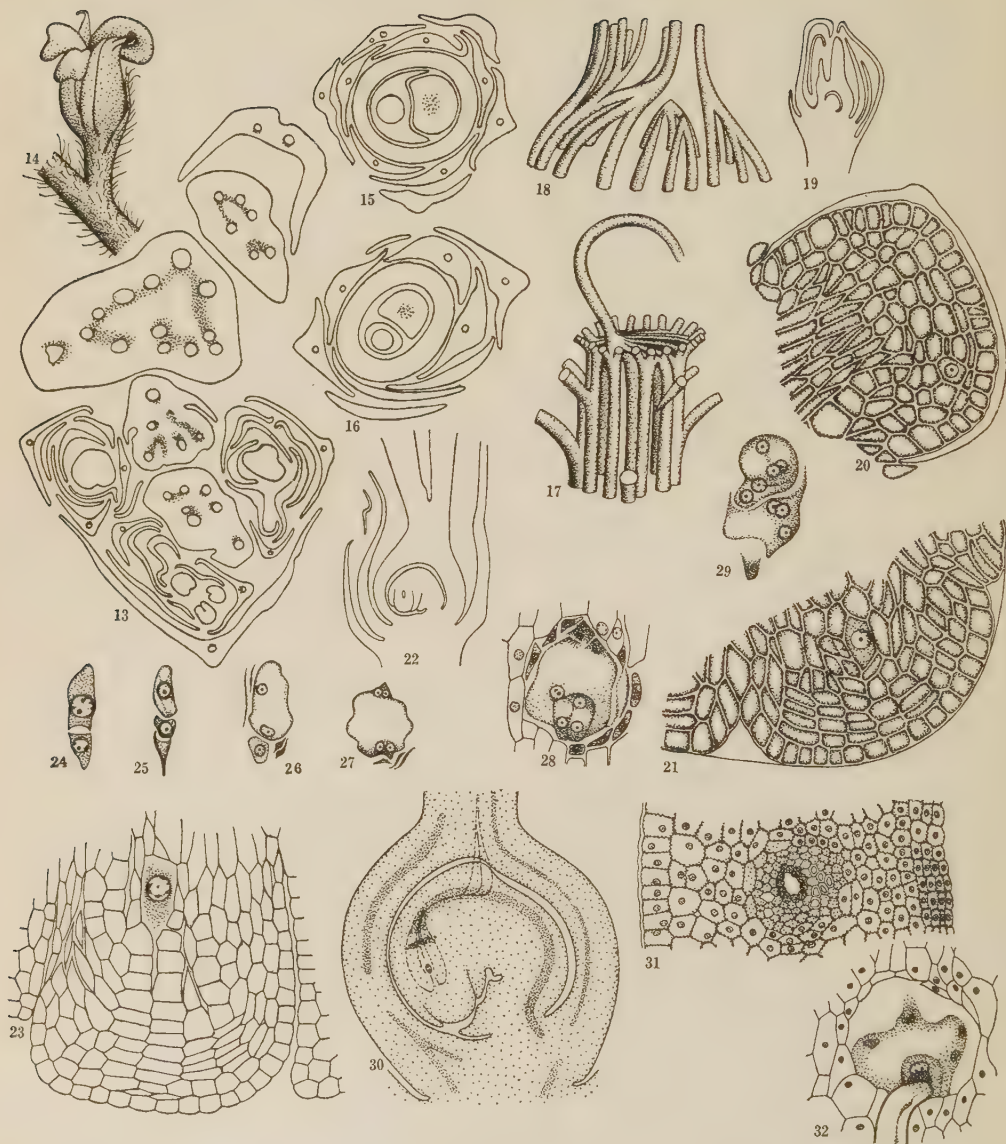
FIGS. 13-32 — Fig. 13. T.s. young female flower cluster. × 20. Fig. 14. Female flower. × 8. Figs. 15, 16. T.s. female flowers, oriented with the bracts toward the bottom of the page. × 20. Fig. 17. Vascular system in base of female flower. × 40. Fig. 18. Vascular system in summit of ovary. × 40. Fig. 19. L.s. female bud. × 20. Fig. 20. Ovule, enlarged from Fig. 19. × 320. Fig. 21. Slightly older ovule. × 320. Fig. 22. L.s. female flower. × 20. Fig. 23. Nucellus from Fig. 22 showing megaspore mother cell. × 320. Fig. 24. Megaspore dyad. × 320. Fig. 25. Megaspore with two cap cells. × 320. Fig. 26. Binucleate embryo sac. × 320. Fig. 27. 4-nucleate embryo sac. × 320. Fig. 28. Mature embryo sac. × 320. Fig. 29. Twin embryo sacs imperfectly developed. × 320. Fig. 30. L.s. ovary showing the course of pollen tubes (diagrammatic). × 40. Fig. 31. T.s. ovary wall. × 320. Fig. 32. Embryo sac just after fertilization, the pollen tube entering from below. × 320.

wall begin to enlarge; the ovary grows to the size of a mature fruit in a matter of one month (Figs. 30, 31 are from material collected April 7; Figs. 33, 34 from material collected May 17). Additional vascular elements become mature and the fine canals are converted into broad resin ducts lined by glandular cells. An inner epidermis remains distinct. The cells previously cut off from it become greatly enlarged, chiefly in the radial direction; they become interlocked by the production of irregular outgrowths, from each one past its neighbors; and undergo conversion into stone cells by the deposition of thick walls which become lignified (Fig. 34). The only further change during the maturation of the fruit is the development of the full hardness of the stony endocarp. At any stage much beyond the one which is illustrated, it is impossible to cut microtome sections of material imbedded in paraffin. The fruit is sparsely speckled with minute dark areas whose structure has not been investigated.

DEVELOPMENT OF THE SEED: GROSS FEATURES — While the fruit is growing to full size, the ovule undergoes a very slight development (Figs. 33, 35). The transverse part of the funiculus becomes elongate and straight. Certain details of its outward structure become more evident than before. A flange of tissue about its base becomes prominent; the obturator becomes larger than before; two flanges, one on each side of the horizontal part, become evident. The nucellus becomes conical, and the inner part of the integument grows past its tip to produce a small micropyle. The outer part of the integument, not growing forward, produces on the side of the integument which lies away from the funiculus a distinct transverse ridge. This ridge is continuous with the flanges on the sides of the funiculus. The ridge represents undoubtedly an outer integument, present as a distinct structure in ancestral plants; it is probable that the flanges also represent part of the outer integument. Growth at the end of the funiculus produces rotation of the integument, micropyle, and nucellus, in the sagittal plane: the axis of the nucellus, formerly directed downward, swings past horizontal to diagonally upward.

After reaching the condition described, the ovule undergoes no increase in size, nor any outwardly visible change in structure, during a period of at least ten weeks. At about the beginning of August, the ovule proper (the ovule aside from the funiculus) begins rapidly to enlarge, while the funiculus, by a partial unbending of its proximal curve, lifts it from the floor of the locule (Figs. 40, 43, 46). The proper ovule grows at first in all parts alike, but begins presently to bulge greatly on the lower side, the side away from the funiculus. It is by growth principally on the lower side that the seed comes eventually again to fill the entire locule, as the ovule did at first. In the course of this growth, the micropyle undergoes further rotation, until it faces straight upward on the upper side of the seed, lying not far in a dorsal direction from the chalaza.

DEVELOPMENT OF THE SEED: HISTOLOGICAL FEATURES — During the long period after fertilization and before the ovule begins its rapid enlargement, certain internal changes occur. The hypostase expands by progressive thickening of the cell walls and death of the protoplasts in the cells lying at its margin. The cells of the part of the nucellus, which lies beyond the endosperm toward the micropyle, take on likewise the appearance of mechanical tissue; their walls become moderately thickened and their protoplasts collapse. The endosperm is throughout this period of the appearance of an empty cavity; by due search, one can usually identify a few endosperm nuclei along its sides and a zygote at the micropylar end. The cavity expands to a slight extent. It compresses and digests some of the adjacent cells, and becomes irregular in outline; and the integument and nucellus along its sides grow slightly, with the effect of allowing it more space.

When the ovule begins its rapid enlargement, the hypostase continues its involvement of cells along its margin until it is of the form of a deep cup. Its position is recognizable externally by a darkening of the chalaza (Figs. 43, 46; the arc of heavy stippling in Figs. 41, 44).

Enlargement of the ovule involves continued growth of the integument and nucellus along the sides of the endosperm, principally in the longitudinal and circumferential directions; they do not become very thick. The integument and nucellus persist as distinct bodies of living cells until the final stages of ripening. The boundary between them is indicated by the inner epidermis of the integument, which becomes differentiated as a layer of small darkly staining cells (Fig. 45) extending as far as the margin of the hypostase. Eventually these small cells become thick-walled.

When rapid growth begins, there forms at the surface of the endosperm a definite layer of cytoplasm containing a single layer of conspicuous nuclei and surrounding a large vacuole (Fig. 38). The layer of cytoplasm quickly undergoes division to form a layer of cells about a lifeless space (Fig. 39). The cells grow into the lifeless space (Fig. 41), which is presently eliminated. During this process the endosperm cells divide freely, and they continue to do so during subsequent growth.

Zygotes whose nuclei have divided (Fig. 36) and two-celled embryos (Fig. 37) are first visible just as the rapid enlargement of the ovule begins. The first division of the zygote appears oblique. Nevertheless, a row of three or four cells is formed. Longitudinal divisions take place in all of these cells. These divisions take place most freely in the more distal cells (Fig. 38), but no part of the embryo forms a definite suspensor; all cells derived from the zygote become parts of the definite embryo (Figs. 39, 42).

The curved shape of the ovule or seed, bulged on the lower side and with the chalaza and micropyle pointing upward, develops before the embryo becomes very large; the growing embryo fits within it. The radicle points up into the surviving indurated tip of the nucellus and toward the micropyle. The embryo passes beyond a top-shaped stage (Fig. 42) by elongation of the hypocotyl downward along the end of the ovule which lies toward the large end of the fruit. The cotyledons (mirror images of each other, separated by the median sagittal plane of the ovule) grow out from the summit of the hypocotyl at approximately a right angle, in the direction of the chalaza. By this time, the bulge of the ovule extends below and beyond the proper chalaza, and the cotyledons duly grow into it below and beyond the chalaza. The hypostase becomes spread open and flattened against the upper side of the locule. The first foliage leaves, an opposite pair decussate with respect to the cotyledons, make their appearance (Fig. 44).

THE MATURE FRUIT AND SEED — Except for the change of its outward colour to turquoise, the pericarp remains at maturity quite as it had been two or three months before. It consists, within its outer epidermis, of a fleshy layer, traversed by meridional bundles containing large resin ducts, together with the hard stone (Figs. 48, 49). There is a small conical point at the top of the stone; in the axis of this point there is a column of soft tissue marking the former course of the pollen tubes.

The seed fills the interior of the stone. The funiculus, flattened against the inside of the large end of the fruit, remains recognizable. The seed coat is a thin layer of crushed cells representing the

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FIGS. 33-49 — Fig. 33. L.s. young fruit. × 8. Fig. 34. T.s. pericarp of developing fruit. × 320. Fig. 35. L.s. ovule soon after fertilization. × 20. Fig. 36. Zygote whose nucleus has divided. × 320. Fig. 37. Two-celled embryo. × 20. Fig. 38. Young embryo and endosperm. × 320. Fig. 39. Embryo and endosperm at slightly later stage. × 320. Fig. 40. Ovule with developing embryo. × 8. Fig. 41. L.s. ovule at about the same stage as Fig. 40. × 8. Fig. 42. Globular embryo. × 320. Fig. 43. Ovule, older than Fig. 40. × 8. Fig. 44. L.s. ovule at about the same stage as the preceding figure. × 8. Fig. 45. Area x enlarged from preceding figure, (endosp, endosperm; nuc, nucellus; integ, integument). × 320. Fig. 46. Older ovule. × 8. Fig. 47. Embryo from same. × 8. Fig. 48. Mature fruit, the outermost tissues dissected away. × 8. Fig. 49. L.s. mature fruit. × 8.
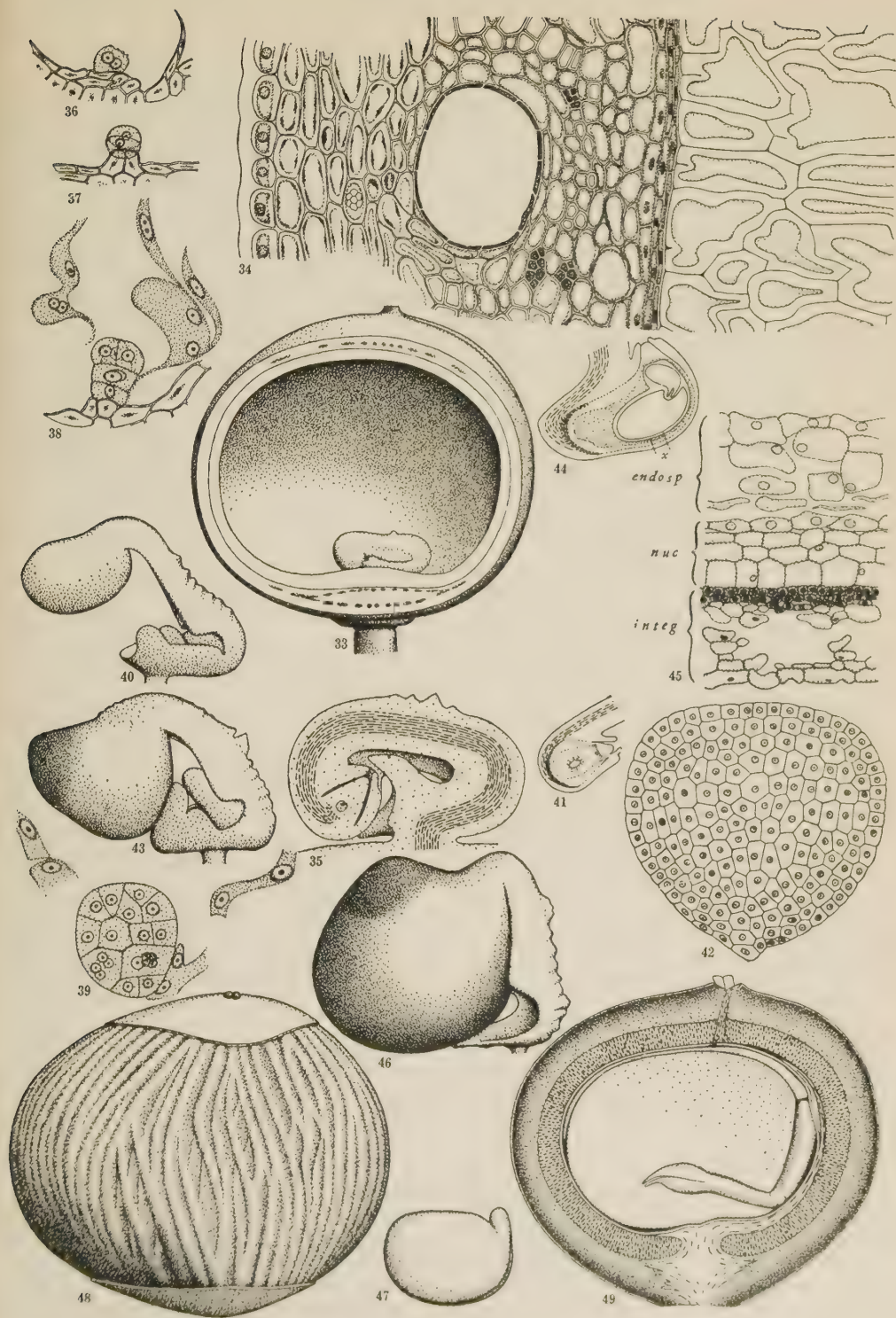
Figs. 33-49.

integument and nucellus. A single layer of small thick-walled cells, the inner epidermis of the integument, can be found in the interior of this layer. Scant bodies of endosperm, pressed against the seed coat, can be found in certain areas. The cotyledons make up the bulk of the seed. They are attached, at their ends toward the larger end of the fruit, to a hypocotyl which runs upward at right angles to their direction. The first internode of the plumule has become elongate, and has carried the first pair of foliage leaves to the interior of the space between the cotyledons.

Remarks

An account such as this, of morphological details in a certain dicotyledonous species, is expected to elucidate the natural place of the species in the system of its family, and the natural place of the family in the system of the dicots. As to the present account, these expectations can be fulfilled only in the future. The Anacardiaceae are a numerous and important family, but mostly tropical, and the embryology has previously been described in reasonable detail in only two species, *Toxicodendron radicans* (Grimm, 1912) and *T. diversiloba* (Copeland & Doyel, 1940). Of a series of studies of *Mangifera indica*, only the first paper (Sharma, 1954) is as yet available. It is my impression that many of the distinctive details here noted are characteristic of the family; for example, the vascular supply to the ovule is identical in *Mangifera*, *Toxicodendron* and *Pistacia*.

The order to which Anacardiaceae is to be assigned has been a matter of disagreement. The families with which Gunderson (1950) grouped it exhibit at least a general similarity. Among them, the small family Julianiaceae agrees with Anacardiaceae in many details; so much so, that one may expect that future classification will include this family in Anacardiaceae. I am not aware that any of the others exhibits similarities of detail which would enable one confidently to point it out as the next thing to Anacardiaceae.

Summary

Pistacia chinensis is a dioecious tree whose inflorescences of both sexes are thyrses.

The male flowers have no perianth. They bear a whorl of a variable small number of stamens whose structure and development are in all respects of the type typical of flowering plants. The tapetal cells become binucleate, then shrivel. The chromosome number (n) is 15. The pollen grains are binucleate, with a finely pitted surface and an equatorial whorl of four or fewer vertical grooves. Pollination is by wind.

The female flower has a variable small number of scale-like perianth segments and a pistil of dorsiventral symmetry with a median stigma above the larger end of the ovary and two lateral stigmas above the smaller end. The ovary contains a single locule and a single basifixed ovule. The funiculus becomes elongate and exhibits various complexities of structure and various bending movements. The ovule including the funiculus forms at anthesis nearly a complete circle; further bending growth turns the direction of the nucellus through inward to directly upward.

The ovule is unitegmous (with traces of a presumedly ancestral bitegmous condition) and crassinucellate. The embryo sac is of normal (Polygonum) type. Fertilization is chalazogamous.

After fertilization, the ovary grows quickly to the mature size and structure of the fruit. The fruit, about 6 mm in diameter, has a stony endocarp derived entirely from the inner epidermis of the ovary.

The ovule exhibits no considerable development until at least ten weeks after fertilization. The endosperm is of nuclear type. The embryo has no distinct suspensor. The mature seed fills the locule of the fruit. The seed coat is a scant crushed layer; scant remnants of endosperm survive. The embryo, and particularly the cotyledons, make up the bulk of the seed. The hypocotyl lies in the large end of the fruit, pointing upward at right angles to the cotyledons.

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THE MORPHOLOGY, GAMETOPHYTE, YOUNG SPOROPHYTE AND SYSTEMATIC POSITION OF *BOTRYCHIUM JAPONICUM* UND.*

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Introduction

Although the earliest studies on Ophioglossales appeared in the middle of the last century, the published work thereafter has been scanty. As their gametophytes are subterranean and dependent on mycotrophy, they could hardly be discovered in natural conditions and their culture in the laboratory could be accomplished only with many difficulties. Apart from Hofmeister's classical study of 1862, Jeffrey (1898) published a paper on *B. virginianum*, Lyon (1905) on *B. obliquum*, and Bruchmann (1906) on *B. lunaria*. Further studies on the morphology and anatomy of the prothalli were carried out by Campbell (1921, 1922) on *B. obliquum* and *B. simplex*, Conard (1929) on *B. virginianum* and Rao (1939) on *B. lanuginosum*.

I have been looking for several years for the gametophytes of Ophioglossales in nature as a prelude towards a study of the life-history and experimental embryology of these plants. With my colleagues

I discovered 15 specimens of the gametophytes of *B. japonicum* with young sporophytes, in Tajimaga-hara, the flooded fields along the River Arakawa, near Urawa, Saitama Prefecture, Japan.

A preliminary report on these studies was published a couple of years ago (Nishida, 1954). At that time there was no published work on the gametophytes of the Ophioglossales in the Far East. Soon after Nozu (1954) announced that he had also found the gametophytes of this species near Tokyo and described their anatomical features. His descriptions are, however, rather vague and lack clearness in certain points. Further, since my observations differ in some respects, I have considered it desirable to publish them in a more detailed form.

Observations

EXTERNAL MORPHOLOGY — All the 15 gametophytes bear young sporophytes, suggesting that they are somewhat old.
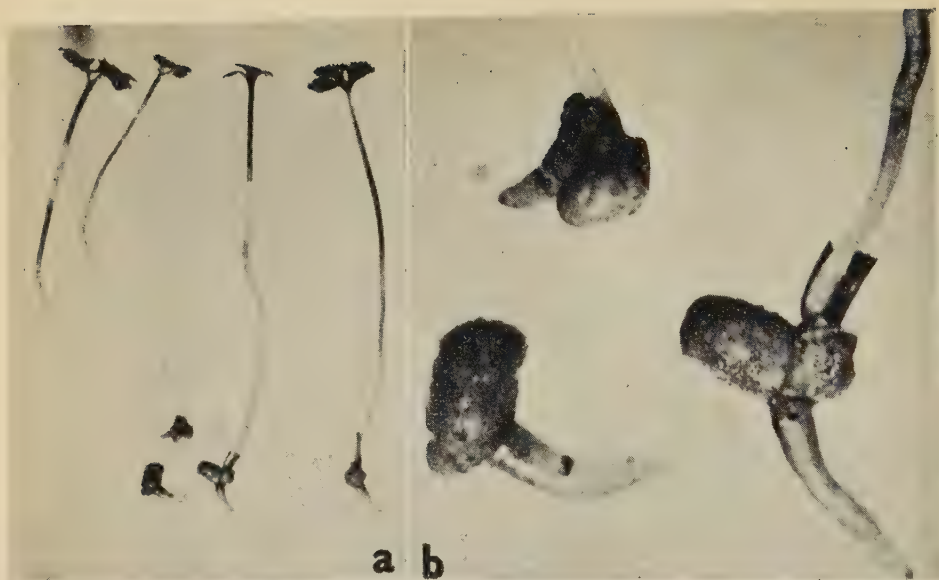
Fig. 1 — Gametophytes of *Botrychium japonicum* Und., with young sporophytes. *a* × $\frac{2}{3}$; *b* ×3.

They are shaped like flattened lumps or clods, or rather like maize grains with a diameter of four to six mm. Some of them are eight to ten mm long (Fig. 1). Every gametophyte bears the first leaf (this is known to appear several years after fertilization). Some bear the second and even the third leaf (they grow in the next and the second year, respectively, after the development of the first leaf). The gametophytes bearing the first leaf are pale or light brown and bear rhizoids over the entire surface while those with the second or the third leaf are dark brown and have fewer rhizoids. The surface of the gametophyte is rough and shows many depressions. Hyphae, belonging to the endogenous mycorrhizic fungi, are often abundant on the surface of the younger gametophytes. *B. virginianum* is described as possessing rhizoids which are generally multicellular (Jeffrey, 1898). In *B. japonicum*, however, I always found the rhizoids to be unicellular.

ANATOMY — The gametophyte is dorsiventral (Fig. 2, a, b). On the dorsal surface there is a longitudinally running ridge bearing the sexual organs. Hofmeister reported that in *B. lunaria* ar-

chegonia were formed on the ventral side and antheridia on the dorsal. Bruchmann (1906), on the other hand, found both types of sex organs on the dorsal side.

Jeffrey (1898) and Campbell (1921) confirmed Bruchmann's observations in *B. virginianum* and *B. obliquum*. In *B. japonicum* also both antheridia and archegonia are developed on and along the dorsal ridge (Fig. 2, a, b).

Antheridia arise irregularly in two or three rows in the uppermost part of the ridge, and archegonia in several rows on the sides or the basal part of the ridge or in adjacent flat areas.

Each antheridium produces more than two hundred spermatozoids, a much larger number than in the Polypodiaceae. It is embedded completely, or sometimes partially, in the gametophytic tissue. According to earlier workers, the antheridial wall is usually two-layered and only rarely three-layered, but I found the latter condition to be frequent in my material. In an old gametophyte, already bearing a sporophyte, archegonia with a perfect internal structure were absent but sperm mother cells or spermatozoids could still

be found sometimes in the antheridia (Fig. 2, c, d). Thus it seems that antheridia may grow and produce spermatozoids even after fertilization is completed and the young sporophyte is developing.

The archegonia comprise four rows of neck cells in six to eight tiers projected vertically from the surface of the ridge, two neck canal nuclei, a ventral canal cell and an egg. All these cells are more
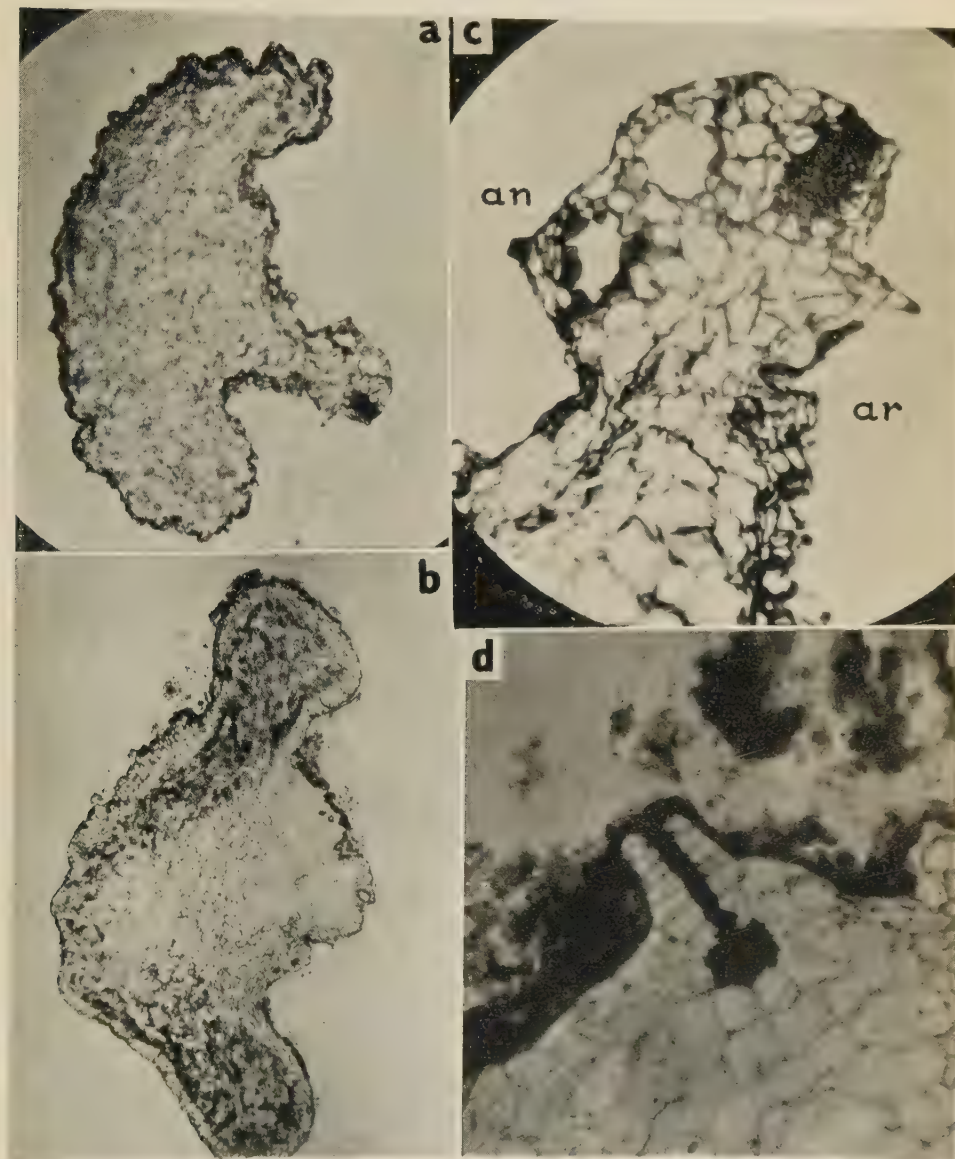
FIG. 2 — (*an*, antheridium; *ar*, archegonium; *rd*, ridge). *a, b.* Cross-sections of gametophytes showing the dorsal ridge on right. × 20. *c.* T.s. gametophyte showing antheridia on the top of the ridge. × 80. *d.* Gametophyte showing archegonium with degenerated contents. × 300.

flattened than those in the Polypodiaceae (Figs. 2, d, 3). Only three or four archegonia with intact egg and the neck canal cells were found in the gametophytes investigated.

The ventral canal cell in *Botrychium* is not easily demonstrated and Campbell (1921, 1922) was unable to demonstrate it satisfactorily in *B. obliquum* but adds that " several preparations indicated that a ventral canal cell or at least a nucleus representing it was present ". His remarks about *B. simplex* are similar. On the other hand, Jeffrey (1898) saw and drew the ventral canal cell in *B. virginianum*. Nozu (1954) mentioned a ventral canal cell in *B. japonicum* but gives no illustration to support this statement.

Only in one case could I see in *B. japonicum* a nucleus which looked like a ventral nucleus (Fig. 3). As most of the archegonia had degenerated, there was naturally little likelihood of seeing the ventral canal cell or nucleus in these old specimens, but it seems probable that they do exist, even if ephemeral, as pointed out by Eames (1936). In cross-section the neck cells are always seen as a chaplet of four cells.

The stem tip of the embryo is directed towards the dorsal side of the gametophyte and the root towards the ventral side. Both break through the tissue of the gametophyte. The root, which has been extended ventrally, reaches the fungous layer where probably it is invaded by hyphae to form the mycorrhiza.

ON EXISTENCE OF THE SUSPENSOR — Only two members of the Ophioglossales, *Helminthostachys zeylanica* and *B. obliquum*, are known to form a suspensor. It is, therefore, interesting to know the conditions in *B. japonicum*.
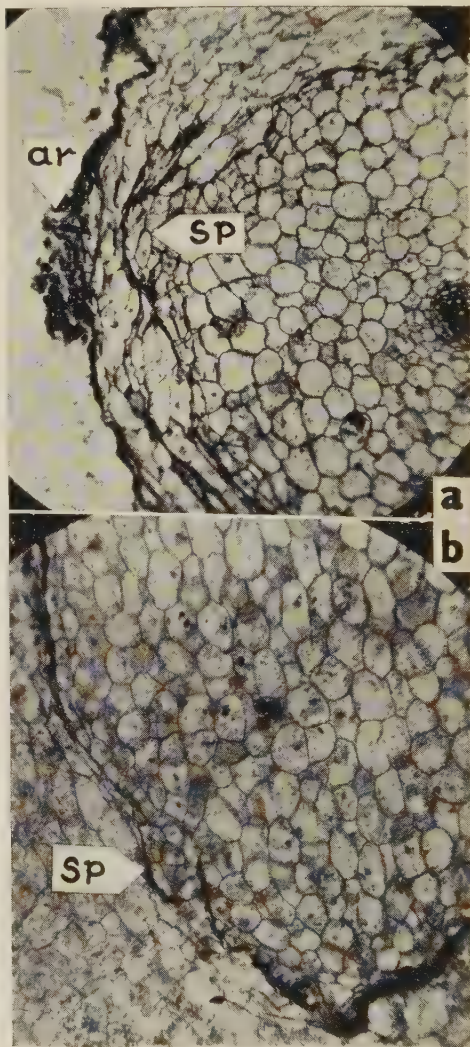
Fig. 4 — Sporophyte (*ar*, archegonium; *sp*, suspensor). T.s. (*a*) and l.s. (*b*) of boundary between stem and root in the sporophyte. × 80.

FIG. 3 — Archegonium with a ventral canal nucleus. × 600.

Serial transverse and longitudinal sections were cut of the young sporophyte imbedded in the tissues of the gametophyte. On the outer surface of the sporophyte there was seen a small parenchymatous protuberance clearly demarcated from the tissues of the stem or the root (Fig. 4). I consider this to be the remnant of a suspensor, because it is always found near the archegonium and is likely to be detached from the sporophyte proper. From serial sections of a somewhat advanced embryo, I could reconstruct a suspensor which was apparently composed of several cells larger than those of the embryo proper (Fig. 5). In Fig. 5c the apical cell can already be seen at the growing point of the shoot. An embryo reconstructed from serial sections is shown in Fig. 5f. In Fig. 5e also we find evidence of a suspensor. According to Campbell (1921) in *B. obliquum* the fertilized egg cell usually becomes elongated and then divides transversely into two halves of which the upper gives rise to the suspensor and the lower to the embryo proper. From my observations I consider that in *B. japonicum* also a suspensor is formed, although convincing proof of its existence through all the developmental stages is lacking.

As for the endogenous mycorrhizic fungus only a few descriptions have been presented so far. The hyphae are said to invade the tissues on the ventral side of the gametophyte. The fungus has not been identified taxonomically, but Jeffrey states that in *B. virginianum* the hyphae have no septa, and form globular bodies similar to the oogonia of Peronosporales. He referred them as " conidia ", neither zoospores nor spermatozoids having been seen in or around them. Jeffrey suggested that the fungus may be allied to *Pythium* or *Completoria*. I often observed the septa in the hyphae, but did not find any globular bodies resembling oogonia or Jeffrey's " conidia ". Further investigations on these endogenous fungi will be reported elsewhere.

Discussion

Nozu (1954) writes that " *B. japonicum* differs from *B. obliquum* in the size of the gametophyte, certain features of the rhizoids, the development of the root and in the projected portion of the archegonia. " In my opinion, however, the gametophytes of both species are generally similar in both size and shape (cf. Fig. 1 and Eames, 1936, his Fig. 85), although the size varies considerably in either species. Nor is there any appreciable difference between the rhizoids of *B. japonicum* and *B. obliquum*, both being invariably unicellular. A characteristic feature of the Ophioglossales is that the development of the first root always precedes that of the first leaf. *B. obliquum*, however, is reported to be an exception, for here the shoot or the leaf appears earlier than the root (Campbell, 1921). Fig. 5c shows the growing point of a shoot and not a root, as it is directed towards the dorsal side of the gametophyte, which is the side of the suspensor.

I could not observe the initiation of the root in my material. In *B. japonicum* also the development of the shoot seems to precede that of the root, as in *B. obliquum*. Thus both *B. japonicum* and *B. obliquum* are similar in their patterns of development. Moreover, the position and orientation of the archegonia are also similar in both: they arise chiefly on the flanks of the reproductive ridge, and sometimes in flat areas on the dorsal surface of the gametophyte.

As Nozu did not give any detailed account of the rhizoids, the development of the root and the projected portion of the archegonia, it is difficult to appreciate the basis of the distinctions drawn by him between *B. japonicum* and *B. obliquum*.

As mentioned before, in external as well as the internal morphology *B. japonicum* closely resembles *B. obliquum* described by Lyon (1905) and Campbell (1921) except that in *B. japonicum* the antheridial wall is frequently composed of three layers instead of two, and its suspensor is composed of several cells even at an early embryonic stage (Fig. 5, a, b), instead of remaining undivided, as in the other species, even after the embryo has grown out of the gametophyte.

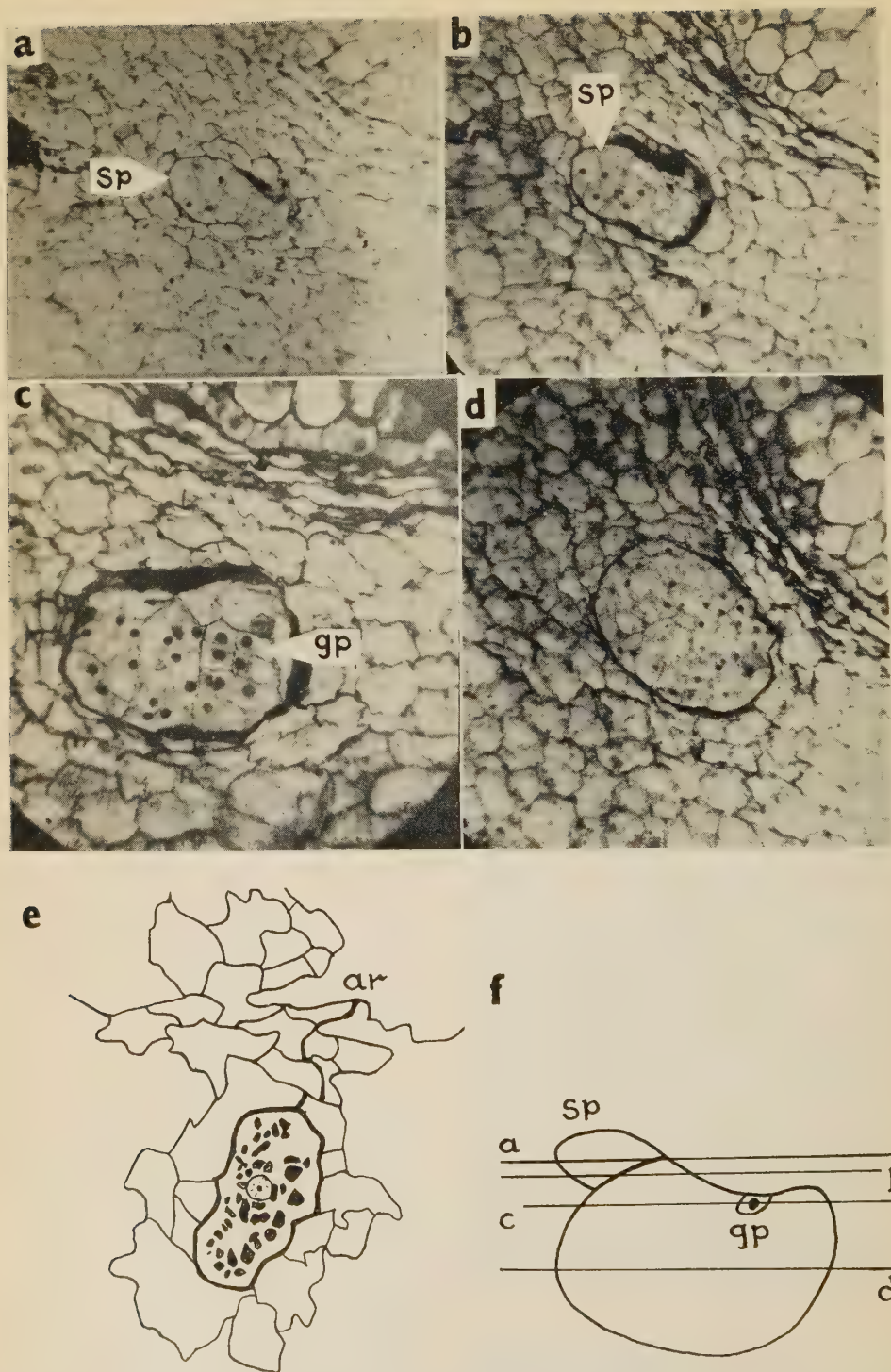Concerning the suspensor, the only figure drawn by Nozu is of a rather vague

FIG. 5 — (*ar*, archegonium; *gp*, growing point; *sp*, suspensor). Serial sections of embryo showing suspensor (in *a* and *b*) and growing point (in *c*). × 300. *e*. Elongation of fertilized egg. × 800. *f*. Diagram of embryo reconstructed from *a-d*.

and dubious type; nevertheless he maintains that " . . . . . . some divisions seem to occur in the suspensor before the embryonal cell divides " and " the suspensor soon increases in size and becomes multicellular . . . . . ". He seems not only to have failed to observe the embryo in the gametophyte, but also to have overlooked the remnant of the suspensor clearly seen by me, in both cross and longitudinal sections.

Cross-sections of the basal part of the phyllomophore[1] of a young sporophyte, which carried an old dark brown gametophyte with a few rhizoids, show the withered remnants of the phyllomophore of the previous year, persisting as a sheath around the phyllomophore of this year. In some specimens the sheath was found to be two-layered. In such cases the sporophyte would be considered to bear the third leaf. *Botrychium* bears usually only one leaf every year.

No gametophyte is found attached to a sporophyte bearing the fourth leaf which is larger than the second or the third. It may have already decayed. It seems that the gametophyte of *B. japonicum* does not survive after the second or third leaf of the sporophyte is withered. According to Hofmeister (1862), the first leaf of *B. lunaria* appears above ground in the second year after fertilization. Therefore, it may be concluded that the gametophyte of *B. japonicum* survives for three or four years after fertilization.

Taxonomical Reference

Lyon (1905) emphasized the presence of the suspensor in the embryo of *B. obliquum* and established a new genus *Sceptridium* to which he transferred all the members formerly placed in the Section Phyllotrichium. *B. japonicum* was also transferred to *Sceptridium*. On the other hand, Eames (1936) does not recognize the suspensor as the diagnostic feature of the genus *Sceptridium*, for it

was only in *B. obliquum* that the gametophyte had been examined. He considers it a specific feature which varies, as also seen in the order Marattiales, within a genus or sometimes even within the same species such as *Angiopteris evecta*. The genus *Sceptridium* would, however, be acceptable in consideration of the vascular anatomy of the phyllomophore (Nishida, 1952a).

B. obliquum is distributed widely in North America and is closely related to the similarly distributed *B. dissectum* Spreng, whereas *B. japonicum* ranges from Japan to Formosa and is closely related to *B. daucifolium* Wall. which is distributed in tropical Asia, Polynesia and India. These two species, *B. japonicum* and *B. obliquum*, thus illustrate two different ranges of distribution of the genus *Sceptridium*. Now that a suspensor has been demonstrated in *B. japonicum*, it can be said that two species of the genus *Sceptridium*, having different ranges, have this structure. Lyon's proposal for using the suspensor as a generic character may, therefore, be considered again.

Summary

A morphological and anatomical study has been made of the gametophyte and young sporophyte of *Botrychium japonicum*.

A small mass of parenchymatous tissue was found on the surface of some of the younger sporophytes and is interpreted as the suspensor, or its remnant.

The gametophyte of *B. japonicum* resembles that of *B. obliquum* which was described by Lyon (1905) and Campbell (1921) in all important respects except that in the former the antheridial wall comprises three layers instead of two.

The gametophyte may continue to grow for three or four years after fertilization.

1. I prefer to designate the so-called " common stalk " of the leaf in Ophioglossales as the " phyllomophore ", for the vascular anatomy of this part suggests that it should be considered stem-like rather than petiolar (Nozu, 1950; Nishida, 1952a).

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THE EMBRYOLOGY OF *DIPTERACANTHUS PATULUS* (JACQ.) NEES

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Introduction and Previous Work

The work on the embryology of the family Acanthaceae was reviewed in 1931 by Schnarf. He refers to the publications of Hofmeister (1858, 1859), Karsten (1891), van Tieghem (1908) and Gigante (1929) on *Acanthus*; Vesque (1878) on *Eranthemum*; Strasburger (1882) and Juel (1915) on *Thunbergia*, and Hartmann (1923) on *Strobilanthes*, *Ruellia*, *Eranthemum*, *Acanthus*, *Crossandra*, *Aphelandra*, *Cryptophragmium*, *Schaueria* and *Beloperone*.

Mauritzon (1934) pointed out the unsatisfactory nature of previous investigations and gave a detailed account of the development of the endosperm in *Ruellia*, *Blechum*, *Brillantaisia*, *Asteracantha*, *Hemigraphis*, *Beloperone*, *Dicliptera*, *Justicia*, *Adhatoda*, *Jacobinia*, *Schaueria*, *Eranthemum*, *Crossandra*, *Acanthus*, *Thunbergia* and *Andrographis*.

Rangaswamy (1941) studied the cytomorphology of *Asteracantha longifolia* and more recently Rao (1953) has given a detailed account of the floral anatomy of several genera.

The present investigation deals with the floral morphology and embryology of *Dipteracanthus patulus* (Jacq.) Nees (Syn. *Ruellia patula* Jacq.).

Material and Methods

Dipteracanthus patulus is a common weed of uncultivated grounds, preferring a shady habitat. It is a small pubescent herb with an erect, branched and straggling stem which often roots at the nodes.

The flowers were fixed in formalin-acetic-alcohol and subsequently stored in 70 per cent alcohol. Sections were cut 5-18 microns thick and stained in Heidenhain's iron-haematoxylin followed by 0·5 per cent alcoholic Fast Green. The seeds were treated with 10 per cent hydrofluoric acid in 70 per cent alcohol for 10-15 days but neither this nor any other treatment gave satisfactory results, and the older stages had to be studied by dissections or hand sections.

Observations

The flower is typically pentamerous, but a few cases of tetramerous flowers with four sepals, four petals, three stamens and two carpels were also observed. A hypogynous nectariferous disc lies just beneath the ovary. In each of the two locules there are eight to ten ovules arranged in two rows on an axile placenta. The style is simple, long and solid. Of the two lobes of the stigma the posterior is greatly reduced. Multicellular, thick-walled epidermal hairs are abundant on the bracteoles, sepals and pistil. The hairs on the ovary become very stiff during fruit formation. The mature fruit is a loculicidal capsule containing five to six seeds with a hairy rim.

FLORAL ANATOMY — The vascular supply to the floral organs was studied from microtome sections as well as from whole mounts of flower buds, cleared in ten per cent KOH and stained with a weak solution of safranin. There is a closed central axial cylinder from which arise the traces going to the various floral organs. The supply to the calyx consists of five midrib bundles alternating with five lateral bundles. After the departure of the sepal traces (i.e. the midrib bundles), and alternating with them, but at a slightly higher level, are given off the five petal traces which divide to form a network in the corolla tube.

In line with the midrib bundles of the sepals arise the five staminal bundles which can be clearly traced over a considerable distance, but the trace meant for the fifth and posterior stamen gradually fades away. The two bundles of each side now supply the respective pairs of stamens and continue unbranched up to the apex of the connective.

There are two dorsal and four ventral bundles in the ovary wall. The placentae and the ovules receive their supply from the ventral bundles. The ovular trace terminates just at the base of the curved embryo sac. There are two bundles in the style which run along its entire length.

MICROSPOROGENESIS — The anther wall consists of four layers: epidermis, endothecium, middle layer and tapetum (Fig. 1). The epidermal cells divide anticlinally to keep pace with the enlarging anther lobe, but later get stretched and flattened (Fig. 3). Next to the epidermis lies the endothecium. Its cells become radially elongated and develop the usual fibrous thickenings (Fig. 3). The middle layer begins to degenerate at the time of meiosis. The tapetal cells contain dense cytoplasm and become multinucleate (Figs. 1, 4, 5). Some of the cells may show as many as five to six nuclei (Fig. 5). Subsequently fusions occur leading to the formation of large irregular polyploid nuclei. With the maturation of the microspores the tapetal protoplasts are absorbed and the walls are obliterated (Figs. 2, 3).

As the pollen grains reach maturity, the partition wall between the adjacent pollen sacs breaks down and they become confluent (Fig. 6). Along the junction of the pollen sacs the endothecial cells lack fibrous thickenings. Dehiscence occurs along this region (Fig. 7).

The microspore mother cells are filled with dense cytoplasm and contain multinucleolate nuclei. As they prepare for meiosis, the cytoplasm secretes a special mucilaginous sheath inside the original mother wall.

The reduction divisions are simultaneous as no cell plate is laid down after Meiosis I. During Meiosis II, the spindles may be arranged parallel or at right angles to each other. Secondary spindle fibres appear after the telophase. Quadripartition takes place by centripetally advancing constriction furrows followed by wedges of the mucilaginous wall which meet in the centre (Fig. 8). The microspore tetrads are usually decussate (Fig. 9) or isobilateral, sometimes tetrahedral.
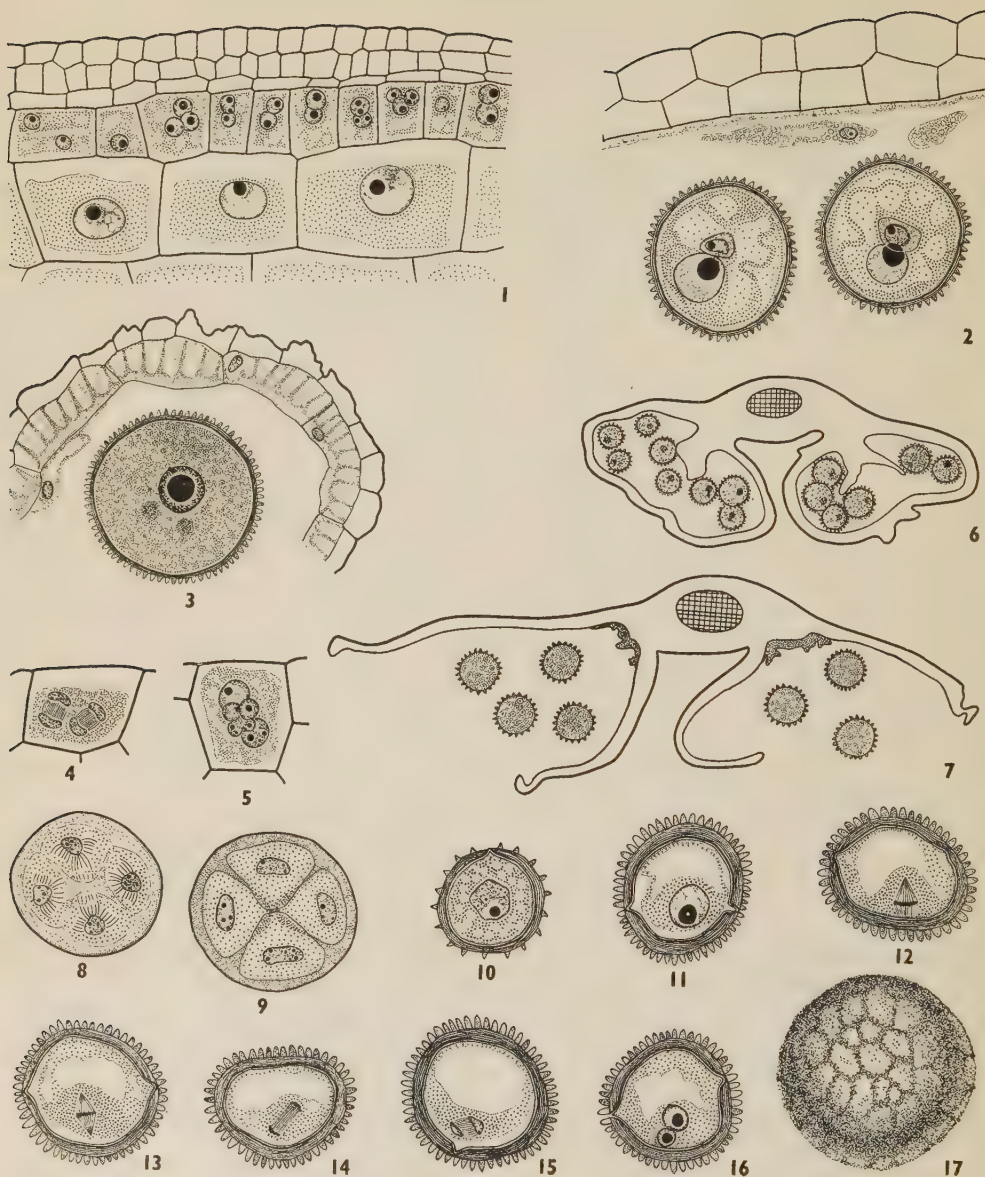
FIGS. 1-17 — Fig. 1. Part of l.s. anther lobe at microspore mother cell stage to show wall layers. × 500. Fig. 2. Same, at bi-celled stage of pollen grain; the middle layer and tapetum have degenerated. × 500. Fig. 3. Anther wall at maturity showing endothecium; owing to dense food materials, the male nuclei could not be made out in the pollen grain. × 500. Figs. 4-5. Mitotic divisions and nuclear fusions in tapetal cells. × 500. Fig. 6. T.s. anther at bi-celled stage of pollen grain (diagrammatic). × 83. Fig. 7. T.s. dehisced anther (diagrammatic). × 83. Fig. 8. Quadripartition of microspore mother cell by furrowing. × 500. Fig. 9. Decussate tetrad. × 500. Figs. 10, 11. Uninucleate pollen grains at young and old stages. × 500. Figs. 12-15. Division of microspore nucleus. × 500. Fig. 16. Two-celled pollen grain. × 500. Fig. 17. Mature pollen grain showing sculpturing of exine. × 300.
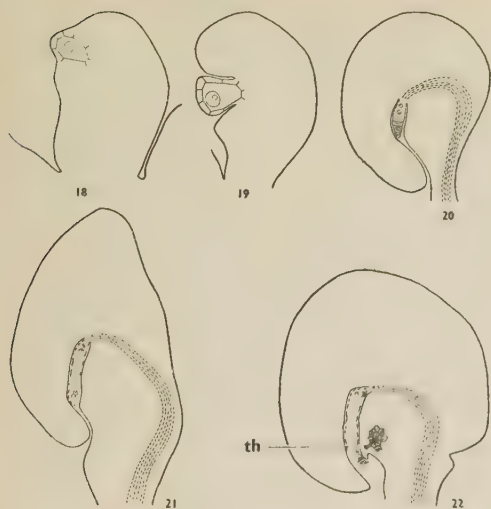
FIGS. 18-22 — L.s. ovules showing progressive development and curvature (diagrammatic). In Fig. 22 the cells marked *th* form a patch of spirally thickened elements in the integument. × 92.

The special mucilaginous wall initially laid at the microspore mother cell stage is now gradually absorbed. This is followed by the breaking down of the original mother wall resulting in the release of the young microspores[1].

MALE GAMETOPHYTE — The wall of the microspore becomes differentiated into a thick exine and a thin intine (Fig. 10). The former can be further demarcated into an outer papillate layer and an equally broad inner striated layer (Fig. 11). Figure 17 shows the exine in surface view. As the microspore enlarges, a large vacuole appears in the centre pushing the nucleus towards the wall (Fig. 11). The first division gives rise to a larger vegetative and a smaller generative cell (Figs. 12-16). The wallward pole of the spindle may be flattened or pointed, and both the conditions can often be observed in the same loculus. Similar instances of symmetrical as well as asymmetrical spindles have been reported in *Podophyllum* (Darlington, 1936).

1. Gigante (1929) points out that in *Acanthus mollis* the pollen sac is filled with a gelatinous mass secreted by the tapetal cells.

The generative cell shows a clear cytoplasmic sheath. It is at first situated close to the wall, but later moves in and comes to lie near the vegetative nucleus (Fig. 2).

Due to the presence of food materials it often becomes difficult to locate the male nuclei in the pollen grains. Attempts to grow pollen grains on culture media were unsuccessful.

MEGASPORANGIUM — The single integument makes its appearance shortly after the differentiation of the archesporium (Fig. 18). The ovule becomes completely
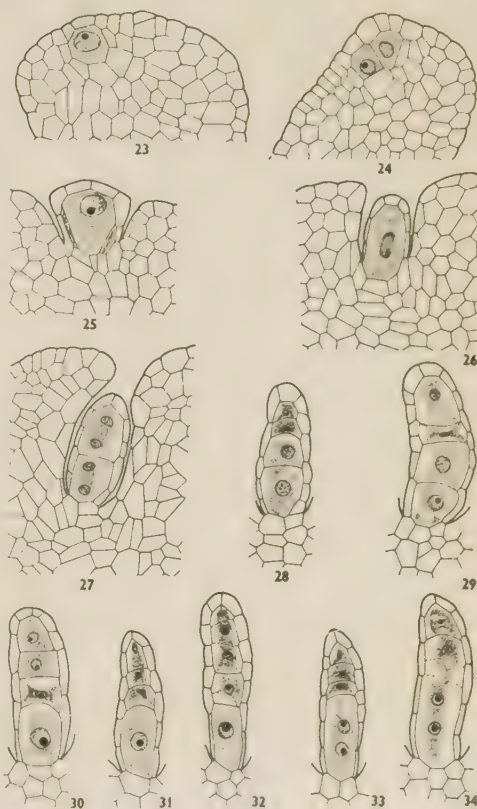
FIGS. 23-34 — Fig. 23. L.s. young ovule showing hypodermal archesporial cell. × 340. Fig. 24. Same, two-celled archesporium. × 340. Fig. 25. Megaspore mother cell. × 340. Figs. 26, 27. Telophase of Meiosis I and II. × 340. Fig. 28. Linear tetrad; the upper two megaspores are degenerating. × 340. Figs. 29, 30. Degeneration of second and third megaspores respectively. × 340. Figs. 31-34. Abnormal tetrads; explanation in text. × 340.

anatropous at the tetrad stage (Figs. 19, 20). At the mature embryo sac stage the integument is very massive consisting of many layers of cells. Some of the integumentary cells (marked *th* in Figs. 22, 39, 40) develop spiral thickenings and resemble tracheidal elements. In later stages the walls of these cells become greatly thickened (Fig. 40) and the whole patch appears dark brown due to certain chemical deposits (Figs. 42, 44, 46, 48).

The nucellar epidermis remains intact up to the formation of the two-nucleate embryo sac (Figs. 33, 34). As the latter enlarges, the nucellus shows signs of degeneration first on the sides and later towards the micropylar end. By the time a four-nucleate embryo sac is formed, the nucellus breaks down completely (Fig. 21). An integumentary endothelium is not formed. The funicular vascular strand extends as far as the base of the embryo sac (Figs. 20-22).

MEGASPOROGENESIS — The hypodermal archesporium consists of two cells although a single cell was also observed (Figs. 23, 24). A single cell has been reported in *Acanthus illicifolius* (Karsten, 1891), *A. mollis* (Gigante, 1929), and *Asteracantha longifolia* (Rangaswamy, 1941). The archesporial cell functions directly as the megaspore mother cell (Fig. 25) and produces the usual dyad and tetrad stages (Figs. 26-30). Usually the upper three megaspores degenerate and the chalazal megaspore functions. The sequence of degeneration may, however, vary. In Fig. 28 the two upper megaspores have

collapsed, while in Figs. 29 and 30 the second and third megaspores are the first to degenerate.

Sometimes more than three degenerating cells were observed above the functioning megaspore (Figs. 31-34). This unusual appearance may either be due to a division of one of the megaspores of the tetrad or to the degeneration of an undivided megaspore mother cell situated above the functional mother cell.

FEMALE GAMETOPHYTE — The divisions of the nucleus of the functional megaspore take place in the usual way resulting in the two and four nucleate stages (Figs. 35-38). The two micropylar nuclei are larger and spherical, while the chalazal are somewhat smaller and irregular in outline (Fig. 38).

The mature embryo sac shows the egg apparatus, two polar nuclei and three antipodal cells. The egg apparatus is somewhat laterally situated and consists of two synergids and egg (Fig. 41). As a rule one of the synergids degenerates before fertilization (Fig. 43), but sometimes it may persist and even become hypertrophied (Fig. 49). The other synergid is destroyed by the incoming pollen tube (Fig. 45). The polar nuclei are usually of similar size, but in one case the lower polar nucleus was found to be much smaller than the upper (Fig. 43). The antipodal cells degenerate soon after fertilization (Fig. 45) and occasionally even earlier. Ephemeral antipodal cells also occur in other plants of this family (*see* Schnarf, 1931; Mauritzon, 1934)

→

FIGS. 35-49 — (*an*, antipodal cells; *ce*, caecum; *pt*, pollen tube; *s*, syngamy; *th*, spirally thickened integumentary cells; *tp*, triple fusion). Fig. 35. Two-nucleate embryo sac. × 454. Figs. 36-37. Both nuclei undergoing division. × 454. Fig. 38. Four-nucleate embryo sac. × 454. Fig. 39. L.s. ovule at mature embryo sac stage (diagrammatic). × 454. Fig. 40. Magnified view of integumentary cells marked *th* in Fig. 39. × 454. Fig. 41. Organized embryo sac. × 454. Fig. 42. L.s. ovule showing formation of caecum at the chalazal end of the embryo sac (diagrammatic). × 45. Fig. 43. Mature embryo sac. The polar nuclei are of unequal size, and the antipodals occupy a lateral position due to the formation of the caecum. × 454. Fig. 44. L.s. ovule at the time of triple fusion (diagrammatic). × 45. Fig. 45. Enlarged view of embryo sac from Fig. 44 showing fusion of a male gamete with the upper polar nucleus. It is not certain whether the egg was fertilized ; neither of the synergids was traceable. × 454. Fig. 46. L.s. ovule at the time of syngamy (diagrammatic). × 45. Fig. 47. Enlarged view of embryo sac from Fig. 46 showing syngamy; the large nucleus in the lower part is the primary endosperm nucleus. × 454. Fig. 48. L.s. ovule soon after triple fusion (diagrammatic). × 45. Fig. 49. Enlarged view of embryo sac from Fig. 48. Of the two cells at the upper end, the smaller is perhaps the zygote and the larger is a hypertrophied synergid. × 454.
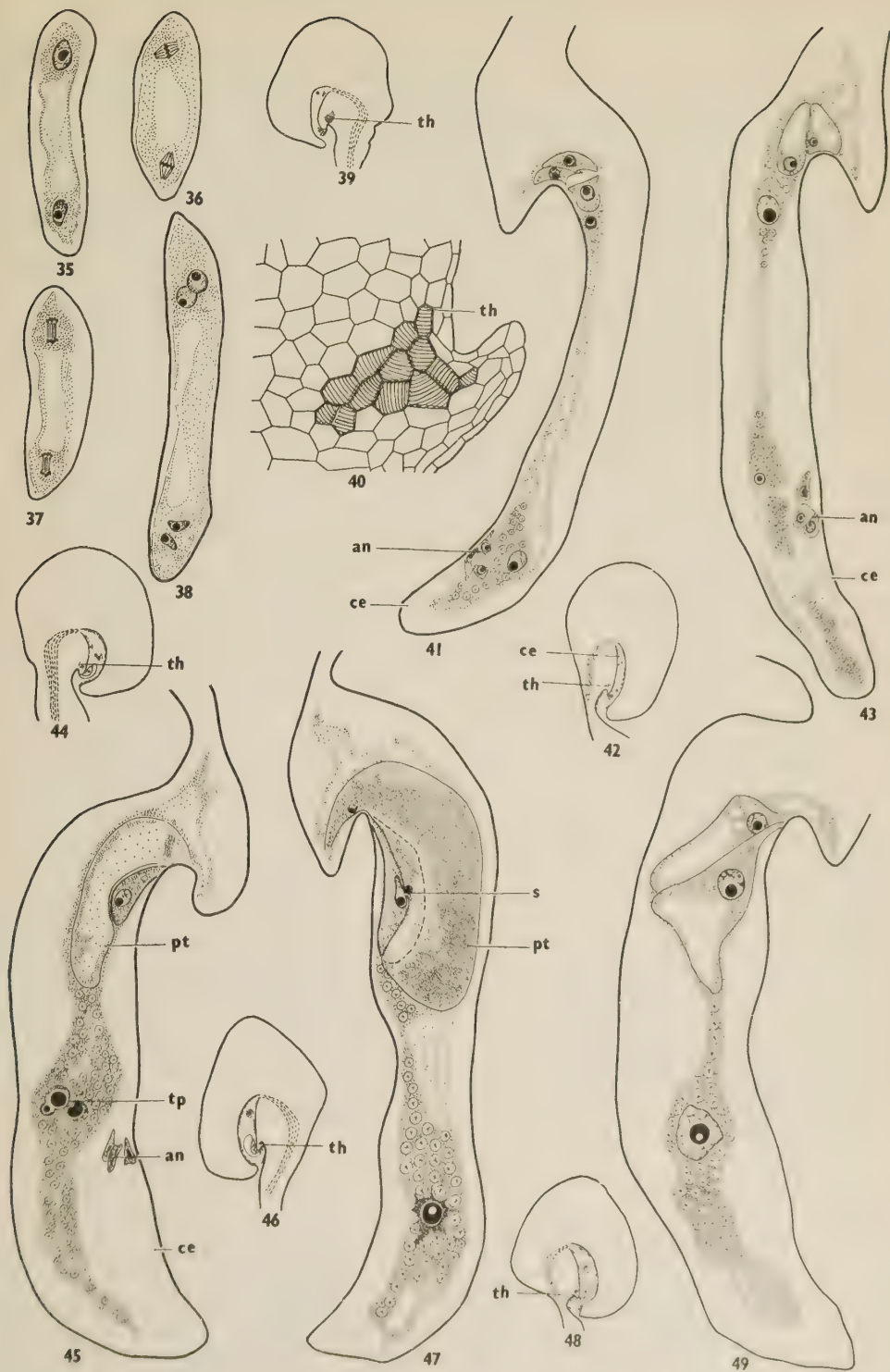
FIGS. 35-49.

and so far the only exceptions are *Aphelandra aurantiaca* (Hartmann, 1923) and *Barleria* (Mohan Ram, 1956), in which they persist until the early stages of endosperm formation.

At the four-nucleate embryo sac stage the nucellus is completely absorbed. As the embryo sac enlarges, it develops a characteristic bend towards the funiculus and its richly cytoplasmic tip protrudes into the micropyle (Figs. 42-49; *see also* Mauritzon, 1934). At the same time the chalazal end of the embryo sac also elongates and forms a caecum leaving the antipodals *in situ* (Figs. 41-43, 45). To the best of our knowledge the caecum has not been reported previously in the Acanthaceae.

The mature embryo sac contains large quantities of starch grains (Figs. 43, 45, 47, 49). They are specially aggregated in the central part so that sometimes the primary endosperm nucleus is masked by them (Fig. 47). The starch is consumed during the development of the endosperm and embryo.

POLLINATION AND FERTILIZATION — The flowers are protandrous and cross-pollination is brought about in the forenoon through the agency of bees.

The style was split into two halves in order to study the course of the pollen tubes. They are long and narrow, their tips swell as they reach inside the ovary, and finally they enter the embryo sacs through the micropyle.

Double fertilization has been observed. In one preparation the polar nuclei had not yet fused and a male gamete was found to be attached to one of them (most probably the upper polar nucleus) (Fig. 45). It was not clear whether the egg had been fertilized in this case. In another ovule a male gamete was lying adjacent to the egg nucleus while the primary endosperm nucleus had already been formed (Fig. 47).

The tip of the embryo sac becomes greatly broadened after fertilization; at the same time the pollen tube swells and becomes very conspicuous. It often shows a darkly staining fragment which may be the degenerated vegetative nucleus (Fig. 47).

The pollen tube persists throughout the development of the seed and was found to lie in close association with the micropylar haustorium (Figs. 62, 63). Whether it is merely a dead structure or has an haustorial role could not be ascertained. Persistent pollen tubes have also been reported in *Cucurbita pepo* (Longo, 1903), *Galinsoga ciliata* (Popham, 1938), *Ulmus americana* (Shattuck, 1905), *Carica papaya* (Foster, 1943), *Oxybaphus nyctagineus* (Cooper, 1949), *Hydrilla verticillata*, *Ottelia alismoides*, *Boerhaavia diffusa* (Maheshwari & Johri, 1950), *Orobanche cernua* and *O. aegyptiaca* (Tiagi, 1951), several members of the Malvaceae (Rao, 1952), and in some other plants.

ENDOSPERM — The primary endosperm nucleus comes to lie in the chalazal part of the embryo sac (Fig. 50) and divides before the zygote. The earliest stage available in our material showed a micropylar chamber with two large nuclei, a chalazal chamber with four nuclei, and a central chamber with six to seven nuclei (Figs. 52, 54). Further free nuclear divisions in the latter are accompanied by its enlargement and the dissolution of the surrounding integumentary cells (Figs. 51, 53, 56). Subsequently most of the endosperm nuclei aggregate in the upper part of the central chamber (Fig. 55). Figure 55 shows that the divisions may not be

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FIGS. 50-57 — (*c*, cellular endosperm; *cc*, central chamber; *ch*, chalazal haustorium; *e*, embryo; *f*, free nuclear endosperm; *mh*, micropylar haustorium; *pt*, pollen tube). Fig. 50. Fertilized embryo sac with zygote and primary endosperm nucleus. × 219. Figs. 51, 55. L.s. ovules soon after fertilization (diagrammatic). × 19. Figs. 52, 54. Magnified views of embryo sacs in Figs. 51, 53. The endosperm shows a two-nucleate micropylar haustorium, four-nucleate chalazal haustorium, and a free nuclear central chamber (endosperm proper). × 219. Figs. 55. Nuclei of the central chamber are aggregated around the proembryo (dissected whole mount). × 219. Fig. 56. L.s. ovule at the stage shown in Fig. 57 (diagrammatic). × 19. Fig. 57. Endosperm showing a cellular and a free nuclear portion, and the micropylar and chalazal haustoria. × 219.
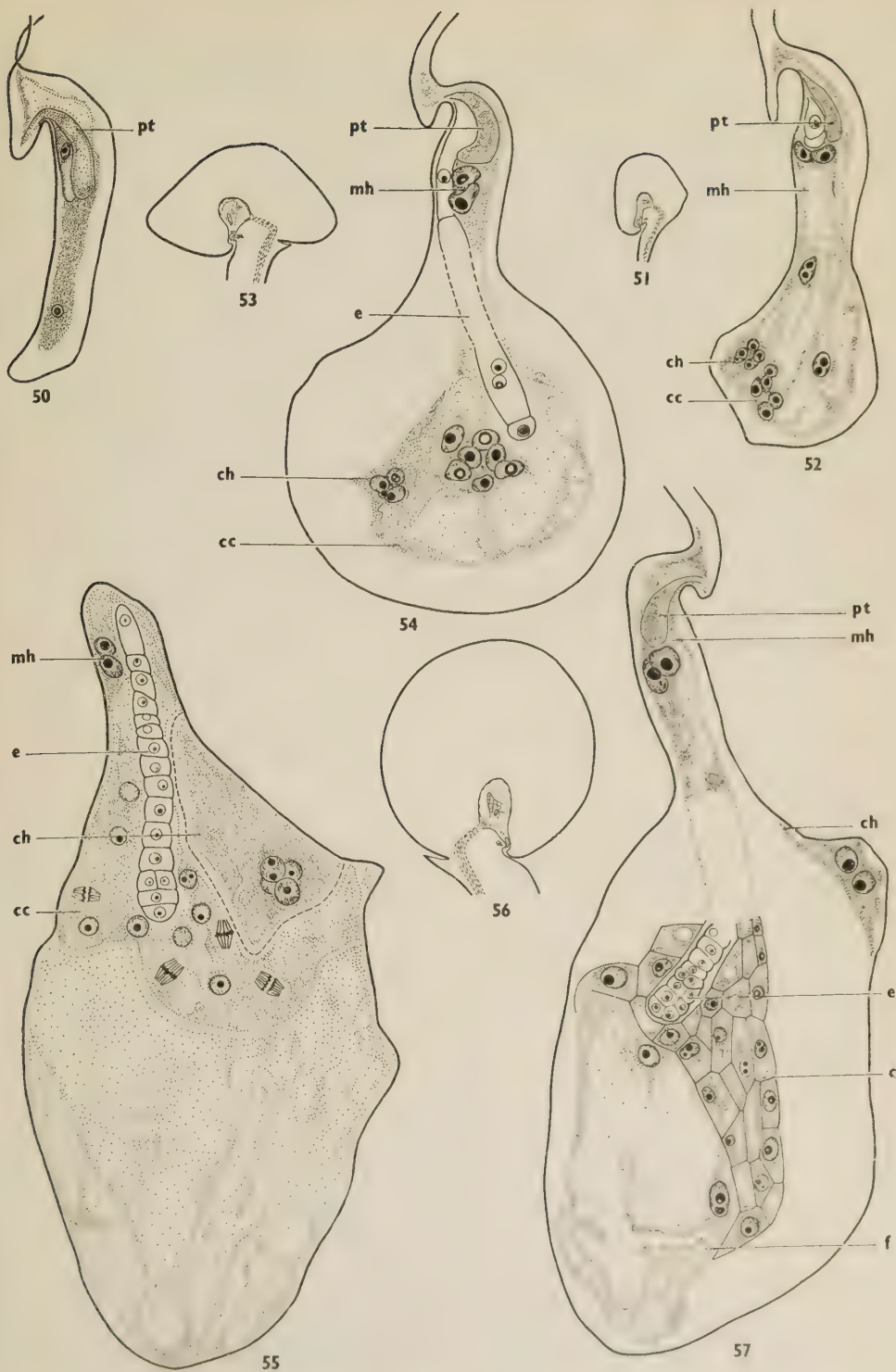
Figs. 50-57.

synchronous; while some nuclei are in metaphase or anaphase, others may be in the resting condition.

When approximately 64 nuclei have been produced in the central chamber, wall formation is initiated in its upper part so that it becomes partitioned into an upper cellular and a lower free nuclear zone (Fig. 57). The cellular zone increases mainly by cell divisions. At the globular stage of the proembryo the cells are thin-walled and vacuolated (Fig. 59). Gradually they become richly cytoplasmic and their walls become uniformly thickened (Fig. 64). The stored food is mostly in the form of oil. The free nuclear part of the central chamber is also richly cytoplasmic and enlarges by absorbing the adjacent integumentary tissue (Fig. 58). Its nuclei become greatly hypertrophied and show conspicuous chromatin lumps (Fig. 60). Ultimately, due to the encroachment of the upper cellular zone, the free nuclear part becomes gradually absorbed and is no longer distinguishable after the differentiation of the cotyledons (Fig. 61).

The micropylar chamber, which is narrow and richly cytoplasmic, has a characteristic bend extending into the micropyle (Fig. 52, 54). The two nuclei usually lie close to the tip of the discharged pollen tube. In one preparation three nuclei were observed (Fig. 63). The micropylar haustorium corrodes the adjoining integumentary cells and is the chief absorptive organ in the upper part of the ovule. Its remnants can be recognized even in the mature seed (Figs. 62, 63).

The chalazal chamber is a small, deeply staining, coenocytic cell, situated at the terminus of the funicular vascular strand (Figs. 56-59). The integumentary cells lying in its vicinity are depleted of their contents and gradually their walls collapse. This activity is at its maximum when the proembryo is progressing from the globular to the heart-shaped stage (Figs. 59, 60). Usually the haustorium contains four nuclei, but frequently only two large nuclei were seen. Probably these had failed to undergo the second division or perhaps they may have been formed by the fusion of four nuclei in pairs

(Fig 57). The chalazal haustorium is originally formed at the chalazal end of the embryo sac. Due to the downward and lateral expansion of the central endosperm chamber, it eventually comes to lie quite close to the micropylar haustorium (Figs. 57, 59, 60). It remains recognizable until the cotyledons are well advanced but is not seen in the mature seed (Fig. 61).

EMBRYO — The zygote divides only after the endosperm has well advanced. It enlarges, becomes vacuolated, and divides transversely to form a terminal and a basal cell (Figs. 65, 66). The latter elongates considerably pushing the terminal cell into the central endosperm chamber.

The basal and the terminal cells undergo transverse divisions forming a filamentous proembryo of three to six cells (Figs. 67-70). The derivatives of the basal cell along with a few daughter cells of the terminal cell constitute the suspensor part of the embryo. The suspensor cells elongate rapidly, become highly vacuolated and sometimes a few of them show a binucleate condition (Figs. 67-69). At the globular stage of the proembryo some of the cells, immediately adjacent to the embryonal mass, divide vertically (Fig. 73) and later the entire suspensor becomes biseriate (Fig. 74). Only in a few cases it remained uniseriate even after the cotyledons had been initiated (Fig. 75). The suspensor reaches its maximum size at the heart-shaped stage of the proembryo but collapses during the maturation of the embryo.

The terminal cell of a multi-celled proembryo, as shown in Figs. 68, 69, undergoes two vertical divisions at right angles to each other and gives rise to a quadrant stage (Fig. 71). This is followed by a third division in the transverse plane forming the usual octant (Fig. 72). Further transverse and longitudinal divisions result in a globular proembryo (Fig. 73). Periclinal divisions in the outermost layer demarcate the dermatogen followed by the differentiation of the periblem and plerome.

The vascular strands differentiate after the cotyledons have been fully formed (Fig. 76). The mature embryo is typi-
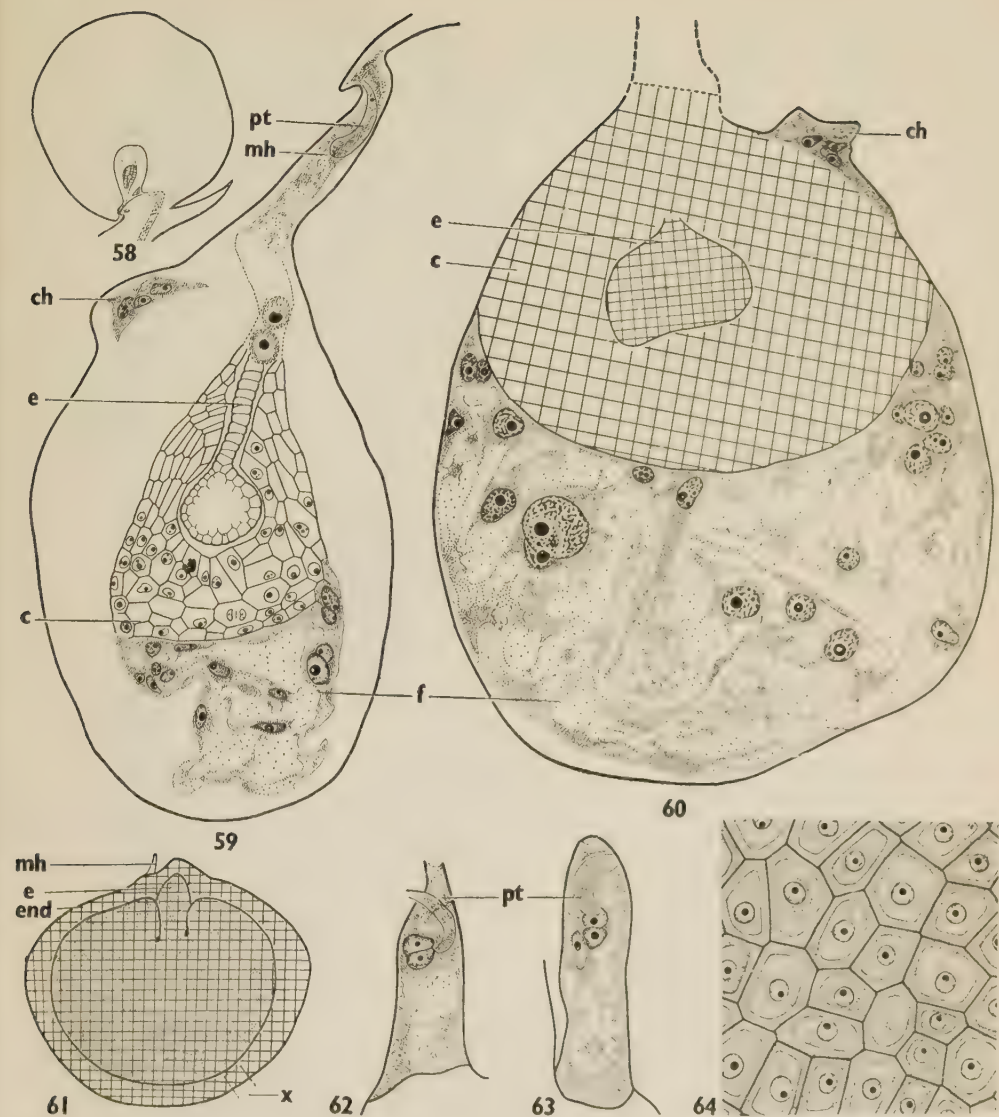
FIGS. 58-64 — (*c*, cellular endosperm; *ch*, chalazal haustorium; *e*, embryo; *end*, endosperm; *f*, free nuclear endosperm; *mh*, micropylar haustorium; *pt*, pollen tube). Fig. 58. L.s. ovule at stage shown in Fig. 59 (diagrammatic). × 15. Fig. 59. Endosperm at globular stage of embryo showing cellular and nuclear portions. × 180. Fig. 60. More advanced stage (from dissected whole mount). × 180. Fig. 61. Endosperm and embryo at maturity; the nuclear portion of the endosperm has been completely absorbed (dissected whole mount). × 10. Fig. 62. Micropylar haustorium marked *mh* in Fig. 61. × 180. Fig. 63. Micropylar haustorium from mature seed. × 180. Fig. 64. Portion of cellular endosperm marked *x* in Fig. 61. × 180.

cally dicotyledonous with two large, flat, leaf-like cotyledons. The embryo consumes the contents of the adjacent endosperm cells which stain very lightly.

POLYEMBRYONY — Normally a single embryo develops from the zygote, but it appears that some of the suspensor cells, lying just above the embryonal mass, can
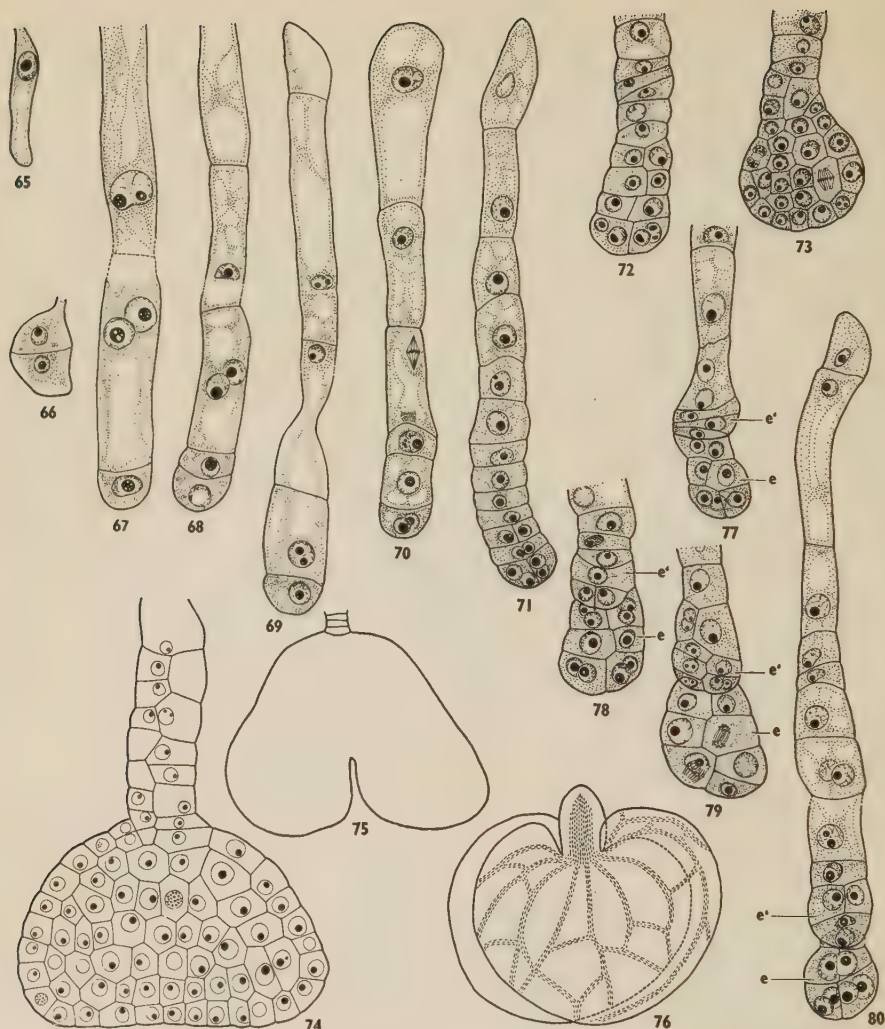
FIGS. 65-80 — (e, embryo; e', additional embryo). Fig. 65. Zygote. × 416. Fig. 66. Two-celled proembryo. × 416. Figs. 67-72. Stages in development of proembryo. × 416. Fig. 73. Globular embryo. × 416. Figs. 74, 75. Stages in differentiation of cotyledons. × 139. Fig. 76. Mature embryo. × 16. Figs. 77-80. Twin embryos (e, and e'). × 416.

proliferate and produce an additional embryo (Fig. 77é). In Fig. 78 the lower suspensor cells have enlarged considerably, and in Figs. 79 and 80 the additional embryo can be easily distinguished from the rest of the suspensor cells as well as from the primary proembryo.

In no case did the additional embryos continue their growth, and ultimately the seed contains only a single embryo.

The only other case of polyembryony in this family is that of *Acanthus mollis* where Gigante (1929) observed a solitary case of three embryos embedded in the endosperm. Their origin was not traced, however.

SEED — The single massive integument consists of many layers of thin-walled cells (Figs. 82, 83). The developing endosperm consumes the adjacent

integumentary cells leaving only four to six layers and at the cotyledonary stage of the embryo only four to six layers remain on the dorsal and ventral sides of the flattened seed (Figs. 90, 91). Of these the inner two layers become sclerenchymatous (Fig. 91). Along the rim two to three layers of cells, lying below the epidermis, remain thin-walled. The next two to three layers consist of thick-walled cells with a narrow lumen. These are followed by three to four layers which are also sclerenchymatous but have a comparatively broader lumen (Fig. 91).

Soon after fertilization the richly cytoplasmic cells of the epidermis elongate radially (Figs. 82, 83). Those on the upper and lower surfaces of the flattened ovule become papillate (Figs. 82, 86, 90), but around the rim they elongate to form long hairs which first appear on the micropylar side. Each hair has a pointed tip, is highly vacuolate and shows a basally situated nucleus (Figs. 84, 88). By the time the cotyledons differentiate, the hairs show spiral thickenings (Figs. 91, 92) and form a tangled mass around the margin of the mature seed. When wetted, they become mucilaginous.

Just behind the rim of hairs, a few epidermal cells of the integument become enlarged (Figs. 86, 87). Like the hairs, their development is also initiated at the micropylar end. At first, they are thin-walled,
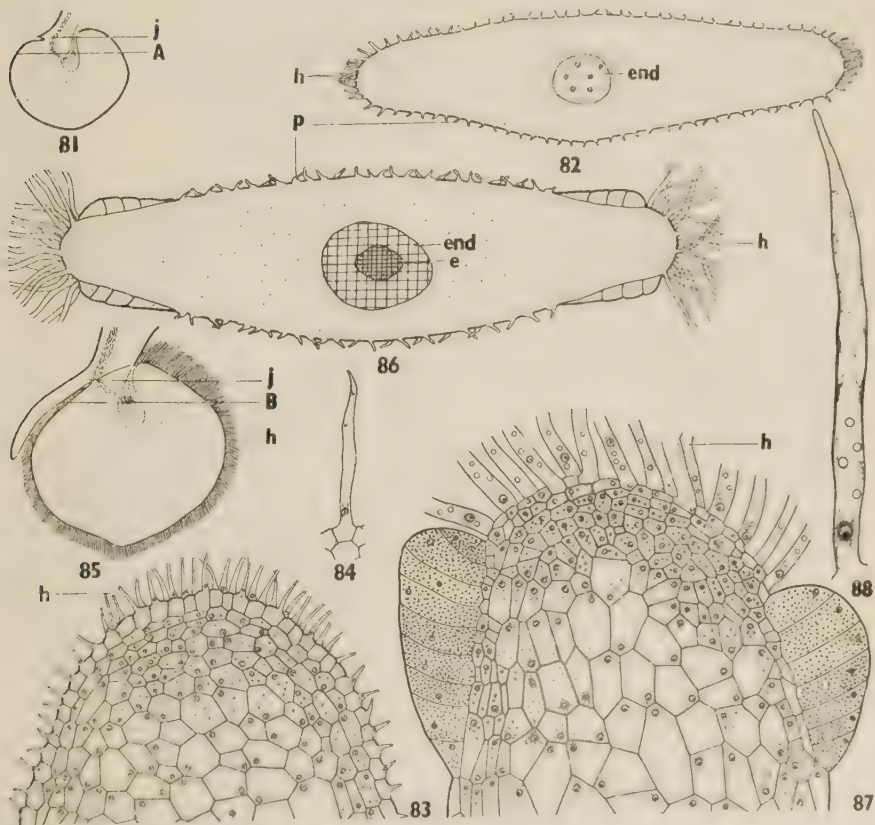
FIGS. 81-88 — (*e*, embryo; *end*, endosperm; *h*, hair; *j*, jaculator; *p*, papillae). Figs. 81, 85. Whole mounts of fertilized ovule and young seed approximately at stages shown in Figs. 54 and 61. × 9. Fig. 82. T.s. ovule at level *A* in Fig. 81. × 36. Fig. 83. Magnified view of marginal portion of Fig. 82. × 164. Fig. 84. Enlarged view of hair from Fig. 83. × 200. Fig. 86. T.s. young seed approximately at level *B* in Fig. 85. × 36. Fig. 87. Magnified view of marginal portion of Fig. 86. × 164. Fig. 88. Enlarged view of hair from Fig. 87. × 200.

but as the seed matures, they become sclerenchymatous and show conspicuous pits on their walls (Figs. 87, 91).

After fertilization, some of the cells of the funiculus, lying opposite to the micropylar end, elongate and form a beak-like structure consisting of thick-walled cells (Figs. 81, 85, 89, 93). This is the ' jaculator '.

Discussion

The main interest in the embryology of the family Acanthaceae has long been centered on the development of the endosperm. Hofmeister (1859; quoted in Schnarf, 1931) described Cellular type of endosperm in *Acanthus spinosus*, while Gigante (1929) reported Nuclear type in another species, *A. mollis*.

According to Mauritzon (1934), who studied 16 genera of this family, the first

division of the primary endosperm nucleus is accompanied by wall formation, cutting off a small cell at the chalazal end of the embryo sac. The division of the upper larger cell separates a narrow micropylar cell from a broad central cell. Nuclear divisions occur in all the three chambers, except in two genera — *Crossandra* and *Acanthus*.

Our material did not show the earlier divisions of the primary endosperm nucleus but there is general conformity with the observations of Mauritzon. The micropylar cell is richly cytoplasmic and contains two nuclei which become hypertrophied. One preparation showed three nuclei in the haustorium. In *Barleria*, *Peristrophe* and *Adhatoda* (Mohan Ram, 1956) the number of nuclei in the haustorium varies from two to five. In *Dipteracanthus* as well as in several other genera of the family, viz. *Blechum*,
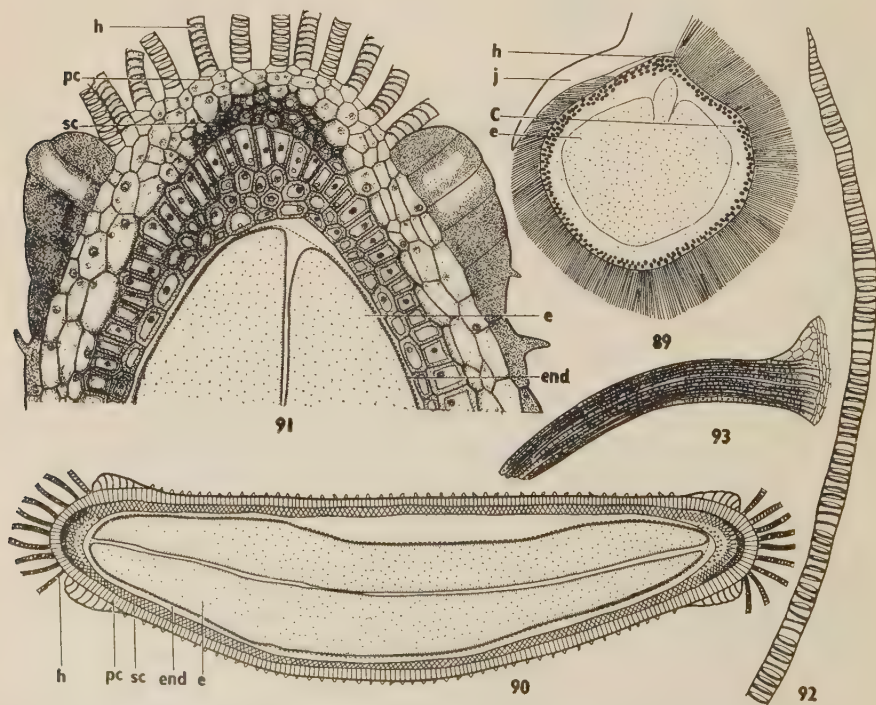
FIGS. 89-93 — (*e*, embryo; *end*, endosperm; *h*, hair; *j*, jaculator; *pc*, parenchymatous cells; *sc*, sclerenchymatous cells). Fig. 89. Surface view of mature seed (diagrammatic). × 8. Fig. 90. T.s. seed at level *C* in Fig. 89 (diagrammatic). × 31. Fig. 91. Magnified view of marginal portion of Fig. 90. × 146. Fig. 92. Hair showing thickenings. × 146. Fig. 93. Jaculator from mature seed. × 104.
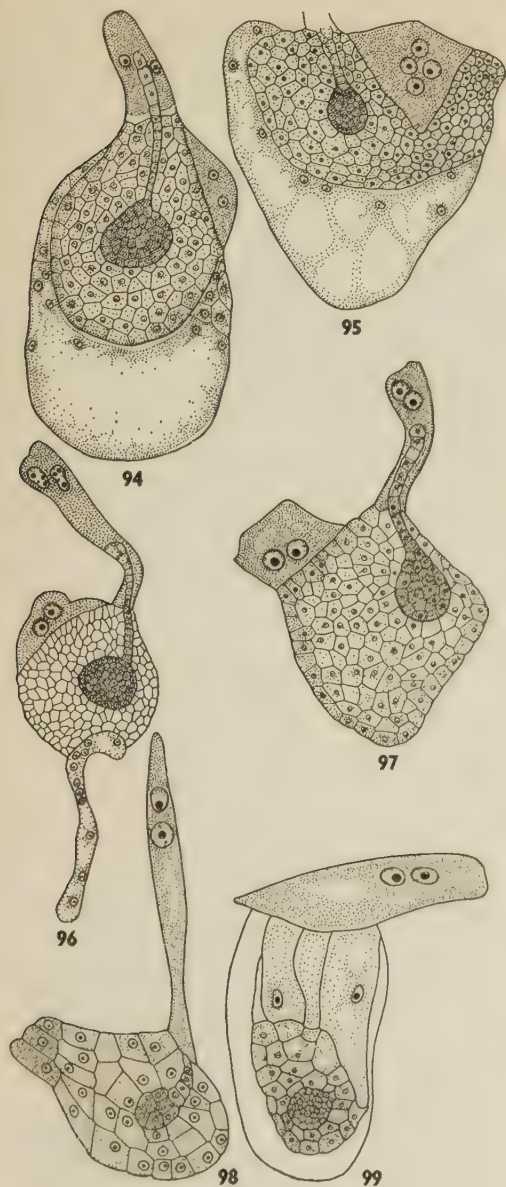
FIGS. 94-99 — Organization of endosperm in various members of Acanthaceae. Fig. 94. *Ruellia pulcherrima.* Fig. 95. *Asteracantha longifolia.* Fig. 96. *Beloperone angustiflora.* Fig. 97. *Jacobinia pauciflora.* Fig. 98. *Crossandra nilotica.* Fig. 99. *Thunbergia reticulata.* (After Mauritzon.) Explanation in text. All × 50, except Fig. 95 × 47 and Fig. 96 × 30.

Jacobinia, Crossandra, Eranthemum, Asteracantha and *Acanthus,* the haustorium is weakly developed and does not extend

much beyond the curved end of the embryo sac. In other genera, viz. *Brillantaisia, Hemigraphis, Beloperone, Dicliptera, Adhatoda, Schaueria,* and in *Ruellia decaisniana* it is more aggressive. Here it not only enters into the micropyle but also penetrates the funiculus and reaches as far as the vascular supply. In *Hemigraphis* and *Ruellia decaisniana* it branches in the funiculus. Mauritzon (1934) makes no mention about the fate of this haustorium. In *Dipteracanthus patulus* it continues to grow for some time and persists in the seed.

According to Mauritzon the chalazal haustorium is four-nucleate in all those genera where the central endosperm chamber is partly cellular and partly free nuclear, namely *Ruellia, Blechum, Asteracantha, Hemigraphis* and *Brillantaisia*; and it is binucleate in those where the central endosperm chamber is completely cellular as in *Beloperone, Justicia, Adhatoda, Eranthemum, Jacobinia* and *Schaueria.* In *Dipteracanthus patulus* the chalazal haustorium does not show any such constancy in the number of nuclei and four or two nuclei occur with more or less equal frequency. A binucleate chalazal haustorium also occurs in *Barleria, Peristrophe* and *Adhatoda,* recently investigated in this laboratory by Mohan Ram (1956). The number of nuclei, we find, is in no way related to the partly cellular and partly nuclear, or completely cellular condition of the central endosperm chamber.

In the central cell of the endosperm, repeated free nuclear divisions give rise to a large number of nuclei. The upper part becomes cellular while the lower remains free nuclear. Mauritzon designates the latter as the ' basal apparatus '. The cellular zone, he says, increases partly by divisions of the existing cells, and partly by the formation of new cells which incorporate some of the free nuclei of the basal apparatus. In *Dipteracanthus patulus* only the former condition seems to prevail and the basal apparatus does not contribute to the growth of the cellular endosperm.

The time of wall formation in the central endosperm chamber varies in different genera and species. In most

species of *Ruellia* it occurs after about 256 free nuclei have been produced. In *R. pulcherrima* (Mauritzon, 1934) and *Dipteracanthus patulus* (present work), however, wall formation commences even at the 64-nucleate stage.

In *Ruellia* (Fig. 94) and *Blechum*, the central chamber quickly extends downwards and the lower part (basal apparatus) is broad and free nuclear. In *Asteracantha* (Fig. 95), *Brillantaisia* and *Hemigraphis* the downward extension takes place more slowly so that the basal apparatus is proportionately smaller. However, in all these cases the two portions are clearly distinguishable from each other. In *Beloperone* (Fig. 96), *Dicliptera, Justicia* and *Adhatoda*, the basal apparatus is represented by a narrow tube containing only a few nuclei. In *Jacobinia* (Fig. 97), *Schaueria* and *Eranthemum* a basal apparatus is absent and the whole of the central endosperm chamber becomes cellular. Cell formation is completed much earlier in *Eranthemum* but is considerably delayed in *Schaueria*. *Crossandra* (Fig. 98) and *Acanthus* represent the final stage in which even the first division in the central chamber is accompanied by wall formation. In these genera the free nuclear phase has been completely eliminated and even the chalazal haustorium is cellular.

Thunbergia is an exception to the above. Here a chalazal haustorium is absent and the micropylar haustorium is cut off after the first division. The uppermost cells of the central endosperm chamber elongate and function as secondary haustoria (Fig. 99).

The type of endosperm development described in the Acanthaceae is not known in any of the related families in the Tubiflorae. Micropylar and chalazal haustoria are no doubt quite common, but between them they include the endosperm proper consisting of a variable number of cells. The free nuclear phase of the central cell and the presence of a basal apparatus are features peculiar to the Acanthaceae. Only in *Phacelia parryi* (Boraginaceae) (Svensson, 1925), there is a somewhat similar condition. Free nuclear divisions occur in all three chambers, chalazal, central and micro-

pylar, but later on they become cellular, and none of them organizes into a haustorium.

There is practically no detailed work on the embryogeny of the Acanthaceae. Gigante (1929) has described the behaviour of the suspensor in *Acanthus mollis*, and Rangaswamy (1941) has figured some stages in the embryogeny of *Asteracantha longifolia*. In *Dipteracanthus* we observed a few cases of proliferation of suspensor cells suggesting the possibility of cleavage polyembryony. However, only one embryo attains maturity. Gigante (1929) has figured a case of polyembryony in *A. mollis* but the origin of the embryos was not traced. Some other plants where the suspensor cells give rise to additional embryos are: *Lobelia syphilitica* (Crété, 1938), *Actinidia chinensis* (Crété, 1944), *Sonerila wallichii* (Subramanyam, 1944) and *Isotoma longifolia* (Kausik & Subramanyam, 1946).

Summary

The pentamerous sub-sessile flowers arise singly or in clusters of two to three. A few tetramerous flowers were also observed.

The anther wall comprises the epidermis, fibrous endothecium, an ephemeral middle layer, and a multi-nucleate glandular tapetum.

No wall is formed after the first reduction division, quadripartition occurs by furrowing, and the resulting microspore tetrads are decussate or isobilateral, rarely tetrahedral. The mature-pollen grains have abundant starch.

The ovules are anatropous, unitegmic and tenuinucellate. The single-layered nucellus is completely absorbed by the time the four-nucleate embryo sac is formed. The latter comes in direct contact with the integument but no endothelium is organized.

The hypodermal archesporium usually comprises two cells, although occasionally a single cell was observed. A parietal cell is not cut off. The megaspore mother cell gives rise to a linear tetrad of megaspores.

The development of the embryo sac is of the Polygonum type. The tip of the

mature embryo sac extends into the micropyle and a ' caecum ' is formed at the chalazal end. The synergids and antipodal cells are ephemeral but occasionally one of the synergids may persist and become hypertrophied.

Double fertilization occurs. The pollen tube is persistent and its remnants are recognizable even in the mature seeds.

The endosperm is of the Cellular type. It comprises a two-nucleate micropylar haustorium, a four-nucleate chalazal haustorium, and a central chamber which becomes separated into a cellular upper part and a free nuclear lower part. The chalazal haustorium collapses after the differentiation of cotyledons, but the micropylar haustorium remains distinguishable even in the seed. During the maturation of the latter the free nuclear portion of the central chamber is absorbed so that only the cellular endosperm persists.

The first division of the zygote is transverse. Both the cells again divide transversely. The derivatives of the basal cell and the upper derivatives of the terminal cell form a long multi-celled, filamentous suspensor. The embryo proper arises from the terminal cell.

In a few cases twin embryos were observed. The additional embryo arises by the proliferation of some of the suspensor cells.

At the time of fertilization the integument consists of many layers of parenchymatous cells. Most of the integumentary cells are absorbed by the developing endosperm. All around the rim the outer epidermis develops characteristic hairs with annular or spiral thickenings. Two or three hypodermal layers become compressed and the next two layers become sclerified to form the hard seedcoat. The funiculus forms a horn-like structure, the ' jaculator ', which aids in seed dispersal.

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REVIEWS

BAILEY, I. W. 1954. " Contributions to Plant Anatomy." Pp. 262. 28 Text Illustrations, and 23 Plates. Chronica Botanica Waltham, Mass., U.S.A. $ 750.

DR VERDOORN'S objective in requesting Professor I. W. Bailey to prepare this book was to draw together and to make more easily accessible certain selections of his works which are representative of the breadth and depth of his scientific interest and also to make better known among students of plant life the many facets of his personality as a botanist and as a scientist. This has been fully realized.

The book is divided into 8 parts with 20 chapters, each with a brief summary at the end. There is a frontispiece photograph of Professor Bailey followed by a biographical sketch by Dr Barghoorn. Then there follows a respectable bibiliography of 113 references published by the author during 1909-1953. Some of these have been reproduced in the text and others have been referred to wherever necessary. At the end there is a collection of 23 beautiful plates besides numerous other illustrations. The book is neatly got up in the characteristic Chronica Botanica style. It is decorated by handsome head-pieces and vignettes especially prepared by the artist botanist Professor B. G. L. Swamy. Some of these are highly significant both structurally and historically, in so far as they attempt to forestall the contents of the pages that follow.

The treatment of the subject matter under such headings as Biochemistry and Biophysics, Entomology, Co-operation in Scientific Research, etc., not only reveals the versatility of the great anatomist but also brings home to us the interdependence of one discipline of science upon another. In fact the subject matter of the whole book has been selected and arranged so judiciously as to illustrate rather vividly the successive attempts during the last 50 years or so to bridge the gaps between plant anatomy and other fields of scientific endeavour.

Part I comprising 5 chapters deals with the cytology and ontogeny of cambium and its derivatives. This embodies part of Professor Bailey's classical researches on cambium in gymnosperms and angiosperms carried out during 1919-1931. Herein new light has been thrown on such problems as the plane of division in cambial cells and the presence of a vacuome, etc., and the confusion that existed in the literature concerning these points has been cleared up to a greater or less extent.

Part II comprising the next 6 chapters summarizes investigations on the microstructure, and the histochemical and physical organization of the plant cell wall. These studies, which were begun in 1933-1934 in collaboration with Dr Thomas Kerr, extended over a period of 10 years and resulted in the clarification of controversial interpretations concerning the organization and physical relationships of the cellulose, lignin and other constituents of the plant cell wall. It is undoubtedly a signal tribute to Professor Bailey's depth of vision as an investigator that the " newer techniques developed in very recent years for the study of organic microstructure, especially improvements in X-ray photomicrography and the development of electron microscopy, have confirmed and little altered his interpretation of cell wall structure in woody plants based on optical and histochemical studies."

Part III treats the development of vessels in angiosperms and the evolution of tracheary tissue of land plants. Herein several phylogenetic trends in the origin and specialization of vessels have been brought to light and these being irreversible have been shown to be significantly reliable in phylogenetic considerations. But the author rightly cautions us that for arriving at valid *positive* conclusions

these have to be used in conjunction with other evidence derived from other fields. His conclusion that " comparative and developmental morphology will be more productive of valid generalizations when problems of mutual interests are attacked from a broadened viewpoint of the phylogeny of modified ontogenies in the vascular plants as a whole ", cannot be too strongly emphasized.

In Part IV comprising chapters 14-16, Professor Bailey and his collaborators give us a picture of their concept of the scope of plant taxonomy. In arriving at taxonomic and phylogenetic conclusions regarding the Ranales, a group of plants which they have made their own, they have depended upon the totality of anatomical evidence available in all organs and tissues of the plants. Thus their inferences regarding the new family Degeneriaceae and the Winteraceae and others are very broad-based and hence sound.

Chapter 16 offers a modification of the classical concept of the angiosperm carpel. The primitive carpel is believed to be a stipulate and styleless structure having a broad three-veined conduplicately folded lamina and bearing numerous anatropous ovules on its morphologically upper or adaxial surface rather than along the margins. Notwithstanding the assertion that " the classical concept of an involute carpel with marginal placentation and a localized apical stigmatic surface will have to be modified ", the authors of the suggestion have sagaciously refrained from applying their interpretation to all angiosperm carpels unless much more information is made available.

In chapter 17 Professor Bailey has shown that the relationship between certain insects and plants, particularly *Cecropia*, is not quite so purposeful as has generally been believed. The next chapter deals with the problems in identifying the woods of the Mesozoic conifers and contains pertinent remarks regarding the use of the term ' species ' in that context. In chapter 19 the author discusses at some length the structure of the pit membranes in the tracheids of conifers and their relation to the penetration of gases, liquids and finely divided solids into green and seasoned wood.

The last chapter is based on an exhaustive report — " The Role of Research in the Development of Forestry in North America "— which Professor Bailey prepared jointly with Dr H. A. Spoehr in 1929 after an extensive fact-finding tour in the U.S.A. and in Europe. This is a delightful and profitable reading as much for laymen as for botanists, foresters and silviculturists.

Notwithstanding the diversity of topics covered by Professor Bailey in this volume, there is one common theme that is easily discernible in all his writings. His approach has been phylogenetic throughout and he has always emphasized evolutionary trends or progressive specialization, be it in cells, tissues, organs or plant as a whole. He is essentially a devoted student of angiosperm evolution, one who is keen to gather evidence for it from whatever source it may be possible. His conclusion in this connection that " the morphological gaps between the dicotyledons and monocotyledons and between the angiosperms and all known gymnosperms are so great that attempts to bridge them at present are purely speculative ", illustrates rather vividly his wide-angled approach to the problem.

In a book of this nature which is essentially a restatement of the author's own views and interpretations, the reader may not agree with all that the author stands for. But most of Professor Bailey's conclusions are very broad-based and logical and appear convincing to the present reviewer. It is just in connection with the interpretation of the primitive angiosperm carpels as conduplicate structures that he finds the arguments somewhat wanting. For instance, Professor Bailey's findings do not rule out the possibility of interpreting the laterally extended, crest-shaped stigma, on which the entire conduplicate concept is based, as rather a derived than a primitive condition. The reviewer is thus inclined, though not without much hesitation, to read figures 19-21 on page 171, in so far as they relate to the formation of this laterally extended stigma in the reverse direction.

The book advocates rather strongly a broadened outlook on all morphological problems. It is of special value to those

who do not have access to the original sources of the articles. Even to those who are better placed in this respect it gives a better appraisal and appreciation of a leading morphologist of our times, apart from being a handy reference book on so many diverse topics.

V. PURI

NELSON, E. 1954. " Gesetzmässigkei-
ten der Gestaltwandlung im Blüten-
bereich, ihre Bedeutung für das Prob-
lem der Evolution." Pp. XII +
302, 689 Figs. (230 coloured). Edit.
E. Nelson, Montreux. Sfr. 81.10.

THE above mentioned book has been privately edited with the financial support of the " Schweizerischer Nationalfonds zur Förderung der wissenschaftlichen Forschung " and recommended by such authorities as Prof. Markgraf (München) and Prof. Portmann (Basle).

The author was originally an artist, painter of flowers, especially orchids. This hobby stimulated in Nelson a keen sense of observation regarding variability in colour patterns and later on of such morphological characters as number, position and interrelations of flower organs generally, and in order to understand the scientific background of these observations, he studied botany at some Swiss universities.

The result was a book which is both scientifically interesting and artistically admirable. It describes and pictures the variations in flowers of many families in great detail and is, accordingly, a valuable addition to our knowledge of flower morphology. Numerous morphological problems have been passed in review: phyllotaxis, zygomorphy, resupination, obdiplostemony, epipetalous stamens, homologies of flower parts, peloria and other teratisms, etc.

It is only natural that such observations led Nelson to construct a synthetic picture which might cover all phenomena observed. However, it is here that the author somewhat loses his firm grip on the subject. His theory is intended to be a morphogenetical (ontogenetical and phylogenetical) one. Neglecting the results of palaeobotany (long range phylogeny),

he restricts himself to micro-evolution and yet indulges in homologizations of flower parts. In this way he has developed a physiological theory of (short range) evolution which is very close to Lamarckism. The main agents of evolutionary mechanism are " formative physiological impulses ". This is rather vague and their nature is hardly discussed but it is assumed that positional and nutritional influences exerted by neighbouring organs play an important part in alterations of shape and position which are ultimately stabilized in the genome.

Despite a certain uneasiness, which steals upon the reader — not only on account of the obviously weak basis but because of the somewhat heavy style — it must be admitted that Nelson's reasonings are clear and logically arranged and that many remarkable ideas have been expressed, which arouse the reader's criticism and self-criticism. There is, in Nelson's book, much refreshing originality and daring in throwing over generally accepted opinions and bringing new ones to the fore.

Morphology is an extremely complicated matter and of morphogenesis we know next to nothing. To have shown in so much detail that what we used to call ' characters ' are far more plastic than is recognized in our daily handling of them, and to have drawn the attention to the so far very much neglected physiological possibilities in the concept of evolution, is certainly no small merit which more than make up for a certain lack of insight of long range homologies and some exaggeration of the main theme.

The bibliography, though comprising some 400 titles, is preponderantly German or at least European, and even here it is not complete. The book is of a stout size and beautifully edited, but the price is rather high for a work which is not a handbook or textbook, but a collection of more or less arbitrarily chosen observations linked by a not too well considered theory. Nonetheless, it is worthy of being on the book-shelf of every botanist, interested in phyllotaxis, flower morphology, organogenesis, genetics and physiology (including biochemistry).

H. J. LAM

PARIHAR, N. S. 1955. " An Introduction to Embryophyta. Vol. II (Pteridophyta)." First edition. Central Book Depot, Allahabad.

THE writing of textbooks is a natural urge of teachers, but to give them the desired quality and elegance is unfortunately a serious problem in this country, partly because of the stingy outlook of many of our publishers and partly because of the inability of most authors to present good authentic illustrations of local material.

The author of the present work has certainly made an honest effort to do a good job although the quality of the paper and consequently that of the illustrations could have been better. Concerning the scope of the treatment, it is at present considerably above the requirement of a B.Sc. Pass degree of Indian universities but below that of an Honours degree. In my opinion the inclusion of a few more types like *Psilotum*, *Isoetes*, *Ophioglossum* and *Azolla* would enhance the field of its utility to a larger circle of students. There are a number of printer's devils, e.g. ' sporagium ' for ' sporangium ' (p. 21), ' graduate ' for ' gradate ' (p. 24), etc. There are also a few discrepancies in the figures and many omissions of literature, both Indian and foreign, but on the whole the treatment of the subject is quite creditable.

N. P. CHOWDHURY

LAWRENCE, G. H. M. 1955. " An Introduction to Plant Taxonomy." Pp. 179. The Macmillan Company, New York.

PROFESSOR Lawrence is already well known to students of botany through his previous book entitled " Taxonomy of Vascular Plants " published in 1951. The present work is of a more restricted nature and is meant for students at the college level. The style of writing is clear and lucid and the illustrations are excellent. The scope is illustrated by the following chapter headings: (1) Taxonomy, what it is, its importance; (2) Plant classification; (3) Evolution and units of classification; (4) Plant structures; (5) Collecting and identifying techniques; (6) Nomenclature; (7) Phylogeny and biosystematics; (8) Taxonomy in North America; (9) Important families and their characters. At the end there is an excellent glossary, the best that the reviewer has seen on terms dealing with systematic botany.

P. MAHESHWARI

FUNDER, S. 1953. " Practical Mycology." Pp. 146. Brøggers Boktrykkens Forlag, Oslo; Asia Publishing House, Bombay.

THIS book, the author says, is meant to be a help for those who have not been disciplined in a regular course in botany but are interested in identifying the commonest fungi which they come across during their professional duties as bacteriologists, physicians, veterinarians, biochemists, pharmacists, agriculturists, etc. There are numerous drawings based on J. W. Wilson and O. A. Plunkett's treatise entitled " Practical Medical Mycology ".

The book is divided into three parts: the first dealing with the fundamentals of mycology, the classification of fungi, and laboratory techniques concerned with culture methods; and the second with the microscopic characters of selected members of the Myxomycetes, Phycomycetes, Ascomycetes, Fungi Imperfecti and Basidiomycetes; the third contains a table of classification. In the second part there is a special key for fungi causing human diseases and a section for fungi causing disease in plants. While the latter is far short of the needs of a professional plant pathologist, the author has tried to figure all the common genera (about 60 in number). Whether this attempt will be considered quite successful is not quite certain, for a botanist in India will miss many fungi which are exceedingly common on the crops here.

There is room for further books of this kind giving proper coverage to the more important fungi of a particular country or area.

P. MAHESHWARI

THIMANN, K. V. 1955. " The Life of Bacteria." Pp. 775. The Macmillan Company, New York.

THE advances in our knowledge of bacteriology, specially during the last two decades, have been tremendous in comparison to other biological subjects. This is due to the fact that the bacteria are multifarious in their physiological activities, are easy to cultivate, and can be handled very conveniently. It is natural, therefore, that bacteria are favourable objects of investigation not only with the bacteriologists but also with physiologists and biochemists. This increased interest in bacteria has led to the accumulation of a large body of information during recent years and it has become extremely difficult to fit in the widely scattered experimental facts into one coherent whole.

The aim of the book, in the writer's own words, is " an attempt not only to see bacteriology as a whole — that is as a branch of biology — but also to see it in its perspective as a development from the past and as an active area of modern investigation ". Professor Thimann has succeeded in this task extremely well, and has achieved an excellent synthesis of the factual material.

The book is divided into four parts. Part 1 deals with the morphology and general physiology of bacteria, and is divided into five different chapters, including one on the bacterial cell and its relationship to other organisms. Part 2 is concerned with the role of micro-organisms in the nitrogen cycle. A whole chapter is devoted to the discussion of the biological fixation of nitrogen — a topic which is usually referred to only cursorily in other books on general bacteriology. In Part 3 is discussed the metabolism of carbohydrates with separate chapters on the different kinds of fermentations brought about by various groups of bacteria. Growth and synthesis is the subject matter of the last part which also includes a separate chapter on the evolution of bacteria.

An extensive bibliography is given at the end of each chapter and references of special interest are indicated properly. At the end of the book there are a complete author index, an index of organisms, and a subject index. Tables, graphs, photographs and drawings have been included at various places in the text to clarify and elucidate many facts.

The lucidity and straightforwardness of the style makes the reading of the book an absorbing pleasure. The historical approach, which is so essential to the study and understanding of any science, is evident throughout. Wherever needful, confusing and inconsistent terminology has been replaced by more reasonable nomenclature, as for instance, the names of the intermediary phosphorylated compounds in the dissimilation of hexose. Chemical phenomena, with which most biologists are not very conversant, are properly explained in the text.

Professor Thimann is to be congratulated for bringing about such an excellent synthesis of classical and modern bacteriology.

B. D. SANWAL

PRIESTLEY, J. H. & SCOTT, L. I. 1955. " An Introduction to Botany." Pp. 627. Longmans, Green & Co., London, New York and Toronto. 30s.

AMONG elementary textbooks of botany published in England there are probably few to beat this one. Priestley was known to be an outstanding teacher with a flare for presenting facts in an attractive manner and a balance of judgement. The first edition of the book appeared in 1938, the second edition (1949) was largely the result of Miss Scott's efforts as the senior author died in 1944. The present and third edition is essentially similar to the second except for the incorporation of some recent work on the metabolic aspects of plant physiology.

The most valuable feature of the book is the integration of morphology and physiology and the fact that it helps the student towards a realization of the significance of the facts learned by him and their possible practical bearing. The weakest part is that on Plant Classification comprising 14 pages of which 4 are introductory, as many as 5 are devoted to the Ranunculaceae, and the rest to the Cruciferae and Rosaceae. Other families are not discussed.

P. MAHESHWARI

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PHYTOMORPHOLOGY

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